ACTA SOCIETATIS ZOOLOGICAE BOHEMICAE

Vol. 62

No. 3

1998

ISSN 0862-5247

ACTA SOCIETATIS ZOOLOGICAE BOHEMICAE[1]

Acta Soc. Zool. Bohem. Vol. 62, No. 3	issued 1998 October 30

ISSN 0862–5247 47678

Editor: Karel Hůrka
Executive editor: David Král

Editorial board: Petr Benda, Jan Buchar, Ivo Hodek, Alois Honěk, Jaroslav Hrbáček, Vojtěch Jarošík, František Moravec, Josef Rusek, Jiří Vávra, Zdeněk Veselovský, Jan Zima

Published and distributed by the Czech Zoological Society. Orders should be sent to the Czech Zoological Society, Viničná 7, CZ–128 00 Praha 2, Czech Republic. Print by the Čihák tisk, Štěrboholská 21, CZ–102 00 Praha 10, Czech Republic

Annual subscription (Volume 62, 1998, 4 issues)

Institutional subscription:	Europe:	USD 80.00
	Other countries:	USD 90.00
Private subscription:	Europe:	USD 40.00
	Other countries:	USD 50.00

This issue was supported by the Ministry of Education (MŠMT ČR)

© Czech Zoological Society, Praha, 1998

[1] A *direct continuation of*:
(i) Vol. 1 (1927–1932): Zpráva o činnosti československé zoologické společnosti za léta 1927–1932
(ii) Vol. 2–53 (1933–1989): Věstník československé společnosti zoologické (*Věst. Čs. Společ. Zool.*)
(iii) Vol. 54–56 (1990–1992): Acta Societatis Zoologicae Bohemoslovacae (*Acta Soc. Zool. Bohemoslov.*)

Acta Soc. Zool. Bohem. **62**: 167–200, 1998
ISSN 0862-5247

A generic revision and phylogenetic analysis of the subtribe Trichalinina (Coleoptera: Lycidae: Metriorrhynchini)

Ladislav BOCÁK

Department of Zoology, Palacký University, tř. Svobody 26, CZ-771 46 Olomouc, Czech Republic

Received February 15, 1998, accepted May 13, 1998
Published October 30, 1998

Abstract. The genus group taxa of the subtribe Trichalinina are revised. The concept of Trichalinina is restricted here to the genera *Trichalus* C. O. Waterhouse, 1877, *Eniclases* C. O. Waterhouse, 1879, *Microtrichalus* Kleine, 1921, *Flabellotrichalus* Pic, 1921 and *Schizotrichalus* Kleine, 1926. The genera *Leptotrichalus* Kleine, 1925 and *Diatrichalus* Kleine, 1926 are excluded from Trichalinina and provisionally placed to the tribe Metriorrhynchini as incertae sedis. Several new synonyms are recognized: *Falsoenylus* Pic, 1926 (= *Microtrichalus* Pic, 1921), *Mimotrichalus* Pic, 1930 (= *Diatrichalus* Kleine, 1926), *Villosotrichalus* Pic, 1921 (= *Flabellotrichalus* Pic, 1921). The genus *Falsotrichalus* Pic, 1921 is transferred to the tribe Platerodini and synonymized to *Ditoneces* Waterhouse, 1879 (Erotinae: Platerodini). New genera *Lobatang* gen. n. and *Kassemia* gen. n. are described and classified within Metriorrhynchini. A phylogenetic hypothesis for genera of Metriorrhynchini with shortened first primary elytral costa is proposed. The monophyly of Trichalinina in former sense based primarily upon the structure of elytral costae is discussed. The key for genera with shortened first primary costa is included. Several new species are described: *Lobatang papuensis* sp. n. (New Guinea), *Lobatang acuticornis* sp. n. (New Guinea), *Kassemia oculata* sp. n., *K. rufithorax* sp. n., *K. wauensis* sp. n., *K. sedlacekiae* sp. n. (all from New Guinea). Following new combinations are proposed: *Lobatang sordescens* (Bourgeois, 1900), *Lobatang miserandus* (Kleine, 1939) and *Microtrichalus basipennis* (Pic, 1926).

Taxonomy, phylogenetic analysis, distribution, Coleoptera, Lycidae, Metriorrhynchini, Trichalinina, new genera, new species, new combinations, new synonymies, Oriental region, Australian region

INTRODUCTION

The lycid subtribe Trichalinina is known from approximately 220 species originally placed in 15 genera. They had been classified as a separate subfamily of Lycidae or a separate tribe by Kleine (1926, 1933), respectively. Recently Bocák & Bocáková (1990) lowered the status of this group to the subtribe within the tribe Metriorrhynchini (subfamily Metriorrhynchinae). First representatives of this group were described already by Fabricius (1775, as *Pyrochroa*) from Australia and Boisduval (1835). Later several species were described by Erichson (1842), Blanchard (1856), Kirsch (1875), Macleay (1887, 1888) and Fairmaire (1877). All these authors described limited number of species without any comments to the already known fauna of this group. The authors publishing in the first half of 19th century classified new species within various genera within Lycidae (*Lycus* Fabricius, 1787, *Porrostoma* Castelnau, 1838, *Metriorrhynchus* Gemminger & Harold, 1869, *Xylobanus* Waterhouse, 1879, *Calopteron* Castelnau, 1838).

First genera now included in the Trichalinina were described by Waterhouse (1877, 1879). Waterhouse (1879) also summarized actual knowledge about the Australian fauna. The next attempt to give the review of Australian fauna was the work of Lea (1909). Some 200 species were described by Kleine and Pic in 1920's and 1930's of this century (Kleine 1925, 1926, 1930, 1936, 1939; Pic, 1921a, 1921b, 1923, 1926, 1930) Unfortunately the generic descriptions were based exclusively typologically and the concept of many genera need a revision The research in the group had been completely interrupted after World War II The last record of this group in literature was Pic's description of one Vietnamese species in 1949 The next taxonomical paper concerning with the subtribe Trichalinina were papers of Bocák & Bocáková (1990, 1991) containing the supergeneric revision of the family and the revision of the genus *Eniclases* Waterhouse, 1879

MATERIAL AND METHODS

During this study of Trichalinina, approximately 3,000 specimens from the whole range of this subtribe were examined About 70 per cent of types were studied which represent all types available in lycid collections deposited in British Museum in London, National Museum of Natural History in Paris and Museum and Institute of Zoology in Warsaw Part of types has not been found in Maurice Pic's collection in Paris and these specimens seem to be lost

Both male and female genitalia of all available type specimens were dissected and membranous parts stained lightly with chlorazol black Sclerotized part were put into a drop of dimethylhydatoinformaldehyd on the label which was pined beneath the specimens, membranous parts were stored in a drop of glycerin in a microvial also accompanying the dry-mounted specimen Important diagnostic characters were designed using the ocular grid-screen and are always accompanied with a corresponding scale The terminology of individual body parts follows Brancucci (1980)

The minimum length trees were searched using computer program Hennig86 ver 1 5 (Farris 1988) using Wagner parsimony analysis The procedure of implicit enumeration (*ie*) was used in all analyses and the results obtained by this procedure are certain to be of minimal length All characters were considered unordered and the equal weight was assigned to them Subsequently using *xstep* command the weight was given to each character according to the fit of each character with the tree resulted from the preceding run The weights were reassigned until the characteristics of the resulted trees did not changed This procedure run during the testing of many preliminary versions of the state matrices Polymorphic characters inside of terminal taxa were coded as "–" in the matrix The program Tree Gardener ver 2 2 (Ramos 1997) was used for editing of matrix and control of Hennig86 program The graphic outputs and mapping of synapomorphies were prepared using the Clados ver 1 9 program

The measures of body parts were done by eyes piece scale of the binocular microscope MBS – 10 The following measures were made (1) overall body length from head to the tip of abdomen, (2) width at humeri, (3) length of pronotum at midline, (4) maximum width of pronotum (usually at base, sometimes in the basal third where lateral dents are situated), (5) maximum frontal distance between eyes and (6) maximum diameter of eye (observed in lateral view)

DEPOSITORIES

The following acronyms indicate depositories for specimens used in this study
BPBM – State Museum of Natural and Cultural History, Honolulu, Hawaii (Dr G A Samuelson),
MSNG – Museo civico di storia naturale, "Giacomo Doria" Genova (Dr R Poggi),
SMNS – Staatliches Museum für Naturkunde, Stuttgart (Dr W Schawaller),
ZMPA – Instytut Zoologii PAN, Warszawa (Dr S A Ślipinski),
LMBC – author's collection

PHYLOGENY

Characters used in the generic classification of Trichalinina and other genera of Metriorrhynchini with the shortened first elytral costa

All characters used for the cladistic analysis and the coding of their states are listed below. The character states and their phylogenetic significance is discussed in detail here. The genus *Metriorrhynchus* Gemminger et Harold, 1869 was kept as an outgroup in the processed matrix as a representative of the subtribe Metriorrhynchina which is supposed to be the sister group of Trichalinina Besides, a designation of the genus *Enylus* Waterhouse, 1879 as an outgroup was tested when a hypothesis for unique evolution of shortened first primary costa was adopted in the beginning of this study The presence of several characters shared by *Enylus* and *Diatrichalus* Kleine, 1926 falsified such hypothesis

Character 0 Arrangement of pronotal carinae
0, complete set of carinae forming seven areolae on the pronotum (Fig 34), 1, carinae partly reduced, less than seven well limited areolae on the pronotum (Figs 35 41)

The arrangement of pronotal carinae forming seven fields is the unique synapomorphy of Metriorrhynchini (Bocak & Bocakova 1990) The advanced character states originate through reduction This fact lowers the explanatory power of this character because multiple origin of reduced pattern is possible

Character 1 Number of pronotal fields
0, at least five fields (Figs 34, 36), 1, three fields (Figs 35, 37–41)

All lateral pronotal carinae can be reduced and only one lanceolate areola is then present in the middle of pronotum The various degree of reduction is present within Metriorrhynchini not only in the group of genera with shortened costa but also in several other genera (for example *Hemiconderis* Kleine, 1926, *Bulenides* Waterhouse, 1879 *Xylobanomimus* Kleine, 1926, some species of *Cautires* Waterhouse, 1879) On the basis of preliminary examination of other characters I suppose, that these animals are not closely related to the genera included in the present analysis With data at hand is not possible to decide definitely if the reduction of lateral carinae occurred many times in the group analyzed or the presence of five field on the pronotum in *Schizotrichalus* is a reversion followed by unique reduction in *Eniclases* The character state for *Eniclases* has been coded "0" because the arrangement of carinae is principally different from those, which has one middle lanceolate areola

Character 2 Strengthened pronotal longitudinal carinae
0 absent 1, present (Fig 39)

The complete longitudinal carinae connecting frontal and basal margin as in Fig 39 are strong and this pattern is supposed to be derived directly from the pattern in *Schizotrichalus* (Fig 36) This pattern has not been found in any other group of Metriorrhynchini and is considered to be a unique apomorphy of *Eniclases*

Character 3 Number of fully developed elytral primary costae in the middle of elytron
0 four primary costae in the middle of each elytron 1, three primary costae in the middle of each elytron

The shortening of first primary elytral costa has been believed to be unique apomorphy of Trichalinina (Bocak & Bocakova 1990) The shortening of some costa occurs quite often in unrelated groups of Lycidae (the genus *Bembotarus* Kono, 1932 in Trotinae *Hemiconderis* in Metriorrhynchini) No correlation with any other important character has been found and the zero weight was given to this character by Hennig86 during successive weighting because of lower fit of this character with the tree calculated

Character 4 Secondary elytral costae
0 secondary costae present, 1, absent (Fig 48)

The absence of secondary costae evolved three times within the set of analyzed genera The genus *Schizotrichalus* where I have found besides typical representatives with secondary costae at least one not yet described closely related species without fully developed secondary costae has been scored "–" This character was used by Kleine (1926) and Pic (1930) for separating of the genus *Diatrichalus* or *Microtrichalus* respectively, within Trichalinina Only four species have been classified with *Diatrichalus* so far, but they have been found many other species clearly congeneric with typical *Diatrichalus* The distinction between the presence and absence of secondary costae within this genus is sometimes very difficult because many intermediate stages are present when numerous species are available therefore *Diatrichalus* has been coded as polymorphic ("–")

A bit different pattern is present in *Kassemia* gen n where secondary costae are completely missing and transverse costae are very strong and form regular transverse or quadrate elytral areolae on elytra The state "1" was coded for *Kassemia* gen n

Character 5 Shape of apical part of phallus
0 as wide as in the middle, only in apical part open, internal sac retractable into the phallus (Figs 53–55 61–63), 1 apical part of phallus narrow, only dorsal part developed internal sac freely exposed, not retractable (Figs 56–59)

The state "1" has been coded for genera *Schizotrichalus*, *Eniclases* *Trichalus*, *Flabellotrichalus* and *Microtrichalus* Their genitalia are very typical and different from other members of the tribe Metriorrhynchini These phalli are very uniform within the genera listed above and hardly usable for identification

The genus *Lobatang* gen n has been scored "0" despite in fact open and slender apical part of phallus as in Fig 61 Nearly parallel sided phallus has been found in related species of this genus (Fig 52) The male genitalia of this genus are substantially different and this fact is supported also by an different internal sac and presence of well sclerotized membrane of phallobase which has not been found in *Schizotrichalus* and related genera

Character 6 – Phallus widest in apical quarter often with a ventral process covering the apical opening ventrally
0 no, 1, yes (Fig 53)

The state "1" has been coded for genus *Diatrichalus* whose members share this unique type of aedeagus This is considered to be an autapomorphy of *Diatrichalus*

Character 7 – Independent thorns at the base of internal sac
0, absent, 1, present (Figs 54, 59)

A pair of the sickle-like thorns at the base of internal sac is present constantly in members of the genera *Enylus*, *Trichalus* and *Microtrichalus* Different types of thorns occur quite often in various members of Metriorrhynchini and more extensive comparison of different types of thorns within the subfamily will be necessary The reduction of number of thorns and a stabilization of their position is one possible process supposed in this group Another possibility of their evolution is strengthening of basal part of internal sac Similar structure at base of internal sac has been found in *Kassemia* gen n but the degree of similarity is quite low and therefore internal sac of *Kassemia* gen n has been coded "0" (Fig 63) Two independent thorns at base can be considered to be advanced state evolved twice in the studied group (*Enylus* and *Trichalus* + *Microtrichalus*)

Character 8 – Pigmented sclerotized keel in dorsal part of phallus
0, absent, 1 – present (Figs 56, 57)

The state "1" has been scored for genera *Schizotrichalus* and *Eniclases*, where it is very apparent The genus *Microtrichalus* was scored as polymorphic, because the identical keel was found in the species *Microtrichalus communis* Only the detailed search on the species level in genus *Microtrichalus* can contribute to the accurate understanding of this character

Character 9 – Sclerotisation of internal sac
0, at least partly membranous, 1, fully sclerotized (Figs 52, 61, 62)

The very characteristic sclerotization of internal sac was found in the representatives of the genus *Lobatang* gen n and character state "1" is coded for this genus

Character 10 – Attachment of bases of lateral glands
0, laterally (Figs 65–67), 1, dorsally (Figs 68–70)

The very characteristic dorsal attachment of lateral vaginal glands has been found in the genera *Schizotrichalus*, *Eniclases*, *Trichalus*, *Flabellotrichalus* and *Microtrichalus* and character state "1" has been scored for these genera This character state is considered to be synapomorphy of all genera listed above and has not been observed in any other representative of Lycidae In the genus *Eniclases* the attachment of vaginal glands is shifted to the middle part of, this position has not been found in any other genus of Trichalinina, the very close *Schizotrichalus* does not share this character state (this character in not coded in the matrix) The very robust basal part of glandular ducts and their very close attachment has been observed in the studied species of the genus *Trichalus*

Character 11 Shape of valvifers
0, valvifers long, slender (Figs 64, 67–71), 1, valvifers short, divergent, with apparent membrane connecting middle or subapical part of valvifers with coxites (Figs 65–66)

Valvifers with separated bases, very short and slightly curved, with lateral connecting membrane were found in genera *Leptotrichalus* and *Lobatang* and character state "1" has been coded for these genera This character state is considered to be a synapomorphy shared by these genera *Enylus* has also short valvifers, but their shape is different and lateral connecting membrane is missing, therefore character state "0" has been scored for this genus Other genera of the analyzed set have slender valvifers apparently longer than coxites and they are usually very slender

Character 12 – Lateral pockets on vagina
0, absent, 1, present (Fig 69)

The very characteristic pockets situated more or less closely to the attachment of lateral vaginal glands were observed in the genus *Microtrichalus* and were scored "1" for this genus in the character matrix The function of these pockets is unknown, it can be associated with the lateral vaginal glands Similar structure has not been found in other Metriorrhynchini

Character 13 – Unpaired very slim gland between valvifers
0 absent, 1, present (Fig 69)

Unique slim gland is present in basal part of vagina in *Microtrichalus* This state was scored "1" in the matrix

Character 14 – Fusion of valvifers
0, free or connected basally, 1, connected in H-shape (Fig 64)

The characteristic shape of valvifers was found in studied species of *Trichalus* and this state was coded "1" A bit similar connection of valvifers and the shape of the bases of coxites were found also in *Schizotrichalus*, but valvifers are connected in their basal, the middle of connecting bridge is sometimes partly membranous and valvifers are slim, therefore *Schizotrichalus* has been scored "0"

Character 15 – Length of spermatheca
0, relatively short, lemon-like (Figs 65–66, 68–70), 1, very long, rod-like (Fig 67)

The spermathecae gradually widened in the apical part are common in Lycidae The very long spermathecae without any widened part were found in genera *Kassemia* gen n , *Enylus* and *Diatrichalus* and character state "1" has been coded for these genera

Character 16 – Structure of basal part of spermathecal duct
0, slim, 1, robust (Fig 67)

The very thick basal part of spermathecal duct has been found in *Diatrichalus* and it has been scored "1" for this genus This character state occurs in *Diatrichalus* only and it has been found in species both with present or missing secondary costae on elytra This character state is very probably connected with the very characteristic sclerotization of the internal sac of phallus During copulation nearly whole length of phallus is inserted into the vagina and the internal sac, which is robust and well sclerotized in most species, is at least partly inserted into the spermathecal duct The degree of sclerotization of internal sac varies in different species, but the widening of the base of internal sac has been found in all species studied The special structure of male internal sac was not scored in the analyzed matrix

Character 17 – Length of alacrista
0, alacrista long, slim, apparently longer than scutoscutellar suture, 1, alacrista much shorter, always much shorter than scutoscutellar suture (Figs 44–45)

The very long alacrista has been found in *Metriorrhynchus* All members of the studied group share the much shorter alacrista than scutoscutellar suture This character has not been connected with the ratio between the body length and width and can be useful for classification of the whole subfamily

Character 18 – Length of lateral process of mesoscutum
0, short, 1, long (Fig 46)

The very short lateral processes of mesoscutum were found in *Metriorrhynchus* and much longer in other genera included in the matrix The length of these processes does not seem to be connected with the ability of flying, because all studied species posses well developed wings and exhibit the same ability to fly according to my field observations

Character 19   Shape of hind margin of metascutellum and the presence of metascutellar keel
0, hind margin of metascutellum straight, without keel (Fig 45), 1, emarginate, with keel (Fig 44)

The shallow emargination of the hind margin of metascutellum has been found in genera *Trichalus*, *Microtrichalus* and *Diatrichalus* The cladogram reflecting the independent evolution of this character in *Diatrichalus* and in *Trichalus* + *Microtrichalus* is more parsimonious than other available cladograms

Character 20 – Strength of hind margin of metascutellum
0, hind margin of metascutellum simple, 1, bent, strengthened (Fig 45)

The bent hind margin of metascutellum has been found in *Schizotrichalus* and *Eniclases* and it is scored "1" in the matrix Such shape of hind margin has not been found in other representatives of group

Character 21 – Keel of postnotum
0, present (Fig 44), 1, absent (Fig 45)

The missing keel and much simpler hind margin of postnotum have been found in *Schizotrichalus* and *Diatrichalus* and this character state is considered to be advanced after comparison with the outgroup

Character 22 – Width of mesosternal process
0, wide (Fig 43), 1, narrow (Fig 47)

The extent of the suture between mesosternum and metasternum vary in the studied group and has been coded in the matrix This character has showed the very low consistency index and during successive weighting it has got the zero value

Character 23 – Width of prothoracal basisternum
0, wide (Fig 42), 1, slender

The extremely narrow basisternum with very high longitudinal keel has been observed in *Leptotrichalus* This character is correlated with the next one

Character 24 – Shape of pronotum
0, approximately as long as wide, 1, very narrow (Fig 38)

The very narrow, long pronotum has been found in *Leptotrichalus* and it has been scored "1"

Character 25 – Pubescence of pronotum
0, whole pronotum with pubescence of the same type and density, 1, apparently denser and longer pubescence at lateral and frontal margins

The pronotum of the genus *Villosotrichalus*, as understood by Pic, has long dense pubescence at lateral and partly frontal margins The much shorter pubescence but apparently denser and longer than in other genera with shortened first primary costa has been found also in *Flabellotrichalus* and therefore both genera were scored "1" In the subsequent taxonomic revision the genus *Villosotrichalus* was synonymized and excluded from the data matrix

Character 26 – Shape of male antennae
0 male antennae serrate (Figs 25–32), 1, flabellate, lamellae originate apically at least in antennomeres following antennomere 4 (Fig 21) 2, flabellate, lamellae originate basally in all antennomeres (Figs 23–24) Character states are considered unordered

Three types of male antennae corresponding with the character states given above were found in the studied group For a long time the shape of the male antennae was used by Pic and Kleine for erecting new genera, but this approach is questioned by gradual lengthening of apical parts of antennomeres 3–10 in *Diatrichalus* (some of them were classified by Kleine as *Flabellotrichalus*) and the occurrence of long lamellae in some species of *Eniclases* without any correlation with any other character The long lamellae are correlated with some other character only in *Flabellotrichalus* as understood in taxonomic part of this study The flabellate antennae of *Kassemia* gen n are very different from those of other here reviewed genera and they remind those of some *Cladophorus* Guerin Meneville, 1830, therefore this type was scored "2" in the matrix and, consequently, with the hypothesis of multiple origin of these character states they were considered to be unordered

Character 27 Shape of the apical maxillary palpomere
0, securiform (Fig 19) 1 parallel-sided, more or less obliquely cut at apex (Fig 20)

The shape of palpomeres is a character quite stable within Lycidae, only in the subfamily Calochrominae it is variable within the genus *Calochromus* Guerin Meneville, 1833 and it is used for identification on the species level Two types of apical maxillary palpus have been observed in the here analyzed group The widened to triangular palpomere has been found in the outgroup and in genera *Kassemia*, *Enylus*, *Diatrichalus* and *Trichalus*, other genera have the slender, nearly parallel-sided apical palpomere The slender palpomere is supposed to evolve in *Leptotrichalus* and in restricted Trichalinina with one reversion in *Trichalus*, consistency index 33 expresses lower explanatory power of this character Weight "1" has been associated with this character during successive weighting

Character 28 – Presence of sensilae at the apex of the terminal palpomere
0 sensillae absent, apical margin simple, 1, apparent sensillae present (Fig 19)

The unpigmented and less sclerotized apical part of both apical maxillary and labial palpomere has been encountered in *Diatrichalus* and the occurrence of this structure is unique in Metriorrhynchinae Very similar structure has recently been found in one genus of the subfamily Erotinae and its exact function is unknown

Character 29 – Shape of the outer margin of the mandible in ventral view
0, nearly straight (Figs 4–8), 1, concave (Figs 9–10, 12–13)

The different position of ventral condyle of mandible results in different shape of basal part of outer margin of mandible in ventral view When the condyle is moved to the outer part of mandibular base, then the concave margin is present when mandible observed ventrally The consistency index 50 is a result of hypothesized reversion in *Schizotrichalus* or independent evolution in *Eniclases* and the rest of Trichalinina in a restricted sense

Character 30 – Shape of the inner margin of the mandible and the shape of mandible
0, inner margin twice broken, mandible relatively robust, 1, inner margin continuous, mandible relatively robust (Figs 7, 11) 2, inner margin continuous, mandible very long and slender (Fig 24) Character states are considered unordered

The mandibles of genera *Diatrichalus* and *Enylus* have continuously curved inner margin of the mandible and this shape has not been found anywhere The mandibles of *Kassemia* gen n have also not broken inner line but they are extremely long and they have been coded "2" as an independent character state These states were considered to be unordered, because their multiple origin is supposed

Character 31 – Shape of mandibles
0, slightly curved or sickle-shaped (Figs 4–6, 14 , 1, apical part curved in right angle (Figs 6–13)

The apical part of the mandible curved in right angle has been found in genera *Enylus* and *Diatrichalus* and in Trichalinina as defined here. The outgroup and genera *Lobatang* and *Leptotrichalus* have other type of mandibles and have been scored "0" This character supports the node including *Enylus* + *Diatrichalus* branch together with monophylum of Trichalinina in restricted sense The consistency index of this character was 100 and consequently high weight was associated with this character

Matrix of character states for Hennig86 analysis

	00000000001111111111222222222223
	01234567890123456789012345678901
Metriorrhynchus	00000000000000000000011000-00000
Kassemia	00011000000000010110010000200020
Enylus	11000001000000010110001000000011
Diatrichalus	1101-010000000011111001000001011
Leptotrichalus	11010000000100000110010110010000
Lobatang	11010000010100000110011000000000
Schizotrichalus	1001-100101000000110100000010001
Eniclases	10110100101000000110111000-10101
Flabellotrichalus	11010100001000000110011001110101
Trichalus	11010101001000100111011000000101
Microtrichalus	11010101-01011000111010000010101

RESULTS AND DISCUSSION

The analysis using equal weights yielded 3 equal most parsimonious cladograms, each with 48 steps, a CI of 0.70, and a RI of 0.65. When successive weighting was applied, also three minimum-length cladograms resulted, with length 250, a CI of 0.92 and a RI of 0.90. The strict consensus tree was counted by the procedure nelsen (Fig. 72) from trees after successive weighting and it has the same length and indexes. The strict consensus tree was used in the classification of the group of genera with a shortened elytral primary costa 1.

Despite the variable taxonomical rank the monophyly of the family group taxon based on the shortened first primary costa has not been doubted yet (Kleine 1933, Bocák & Bocáková 1990, 1991). But this hypothesis has been only weakly supported because the shortened costa has been the only character used for a classification of Trichalinina. The reduction of pronotal costae was another character, but it has been known for long that it occurs also in other groups and this reduction apparently evolved many times in Metriorrhynchinae. During the present analysis I have not found any character uniting the remaining Metriorrhynchini as used in classification of Bocák & Bocáková (1990) and they are apparently paraphyletic taxon, when classifying Trichalinina in traditional sense. The genus *Kassemia* gen. n., another Metriorrhynchinae genus with shortened first primary elytral costa, is not more related to other genera with shortened costa than to *Metriorrhynchus*. On the other hand, there are other characters uniting the genus *Enylus* (without shortened costa) with the genus *Diatrichalus*. This finding supports the view that the shortened costa evolved very probably four times (first time in *Lobatang* and *Leptotrichalus*, second time in *Diatrichalus*, third time in restricted Trichalinina and fourth time in *Kassemia* gen. n.). The competitive hypothesis is that shortened costa has evolved once in the whole group and consequently the reversed character state evolved in *Enylus* and more primitive arrangement of pronotal carinae evolved again in *Schizotrichalus* and *Eniclases*.

One important character defining Trichalinina clade in a restricted sense as a natural group (i. e. Trichalinina s. str.: *Flabellotrichalus*, *Trichalus*, *Microtrichalus*, *Schizotrichalus* and *Eniclases*) has been found during analysis. The dorsally attached accessory glands of vagina were found in all genera of restricted Trichalinina. Another character uniting this group of genera is shape of male genitalia, there are always very slender, with exposed internal sac Within this group I have found also a gradual reduction of pronotal carinae from slightly reduced pattern shared with many other genera of Metriorrhynchini (*Schizotrichalus*, modified as in case of *Eniclases*) to only one longitudinal areola This fact would support the opinion that Trichalinina incorporating the above given genera could be one of smaller clade within Metriorrhynchini The extensive search of related genera of *Leptotrichalus* and *Lobatang* gen n and *Enylus* and *Diatrichalus* is necessary for an understanding of the evolution of whole Metriorrhynchinae

If accepted, this point of view will have some substantial consequences of classification of the subtribes within Metriorrhynchini It will be necessary to define Metriorrhynchini with a number of smaller clades one of which would be the restricted Trichalinina (*Flabellotrichalus* + *Trichalus* + *Microtrichalus* + *Schizotrichalus* + *Eniclases*)

The relationship of genera within restricted Trichalinina have remained unresolved Apparently genera *Schizotrichalus* and *Eniclases* are much more related to each other than to the rest of subtribe This view is supported by two synapomorphies (pigmented, sclerotized dorsal keel of phallus and strengthened hind margin of metascutellum) The more primitive arrangement of pronotal carinae, which seems to be unique reversal of *Schizotrichalus* and *Eniclases* in the analyzed set of genera, may change in plesiomorphy if more primitive genera of clades *Leptotrichalus* + *Lobatang* gen n and *Enylus* + *Diatrichalus* with ancestral arrangement of pronotal carinae are found Some characters used in the past by authors for classifying genera within Lycidae (lamellae of male antennae and presence/absence of secondary costae) proved to be unusefull during this analysis These advanced character states evolved many times in the studied group and their significance is much lower than expected The genera *Microtrichalus* and *Trichalus* also showed higher degree of relationships to each other than to any of remaining genera of Trichalinina This hypothesis is based on the presence of a pair of thorns at the base of internal sac This character evolved only once within Trichalinina in the restricted sense and seems to be of high importance More advanced characters are present in *Microtrichalus* (pockets of vagina and unpaired gland at base vagina) The uniquely fused valvifers were found in *Trichalus*

The clades *Leptotrichalus* + *Lobatang* and *Enylus* + *Diatrichalus* were stable during analysis Their branching sequence is supported only by one character (character 31, shape of mandibles) This character unites the clade *Diatrichalus* + *Enylus* with restricted Trichalinina

The clade *Leptotrichalus* + *Lobatang* is based on the shape of valvifers The other apomorphies are not unique for them *Lobatang* has very unique advanced male genitalia, *Leptotrichalus* is defined by his very slender pronotum and basisternum The shape of genitalia is very variable within *Leptotrichalus* and may be useful for infrageneric classification of this group

The clade *Enylus* + *Diatrichalus* is based on shape of spermatheca (shared with *Kassemia* but multiple origin supposed in all cladograms) and the shape on mandibles Searching for their close relatives will be necessary for building of robust hypothesis about their position within Metriorrhynchinae

ZOOGEOGRAPHY

The tribe Metriorrhynchini occurs in the Oriental, Australian, Afrotropical and partly in Palaearctic regions The highest diversity has been found in the Oriental and the northern part of the Australian regions Afrotropical fauna of Metriorrhynchinae is quite poor, especially in genera representation Similarly, the very low level of endemism has been found in the Palaearctic representatives of this subfamily Most of the Palaearctic representatives occur in southeastern China, the ranges of few of them reach Japan and Russian Far East The Australian fauna is very similar to the Oriental one and simultaneously any important similarities between Australian and Afrotropical fauna have not been found. It can be supposed that whole Lycid fauna of Australian Region, 89.7 per cent of which is formed by representatives of Metriorrhynchinae, is of Oriental origin. The present knowledge about the plate tectonics (Crook 1981, Powell et al. 1981) is in the congruence with the phylogenetic hypotheses of relatively recent multiple speciation in Metriorrhynchini and especially Trichalinina and their migration from the old Malesia to the south to Australia.

The Trichalinina s. str. as restricted in the previous phylogenetic analysis (*Flabellotrichalus* + *Trichalus* + *Microtrichalus* + *Schizotrichalus* + *Eniclases*) are limited to the Eastern part of Oriental region and to the Australian region only. Northern limit of its range lies in southern Indochina (central Vietnam to southern Thailand). Only several specimens have been collected in this region and all belong to the genus *Microtrichalus*. Similarly, the Philippines accommodate only several species of *Microtrichalus*. Some representatives of *Microtrichalus* occur on the Sunda islands, but they do not form substantial part of Metriorrhynchini in these areas both in number of species and number of collected individuals. The Lesser Sundas are generally poor in Lycidae fauna because of much drier climate. Few species of *Microtrichalus* occur is western part of the chain according to very incomplete records. The fauna of Moluccas is much more similar to the Papuan one than to the Oriental. Trichalinina are much more common there and besides *Microtrichalus* several *Flabellotrichalus* and one species of *Eniclases* were collected there.

A striking feature of the distribution of Trichalinina is the great richness in both genera and species in the Papuan subregion. All known genera are represented there except *Trichalus*, but its occurrence at least in southern part of New Guinea is very probable. All genera reached much higher diversity here than in adjacent islands. New Guinea is relatively young and it is supposed that first land commenced to appear in New Guinean region at the end of Eocene. In the north situated arc of islands was accreted to the northern margin of Australian plate 15 million years ago and the present size of New Guinea was reached in Pleistocene only (Crook 1981, Powell et al. 1981). It can be supposed that ancestor or ancestors of Trichalini inhabited the easternmost islands of westward moving Sundaland and later they underwent multiple speciation in New Guinea. Similar situation has been documented in the case of plant distribution (Steenis 1979). The small size of Solomon islands and Moluccas can be the reason for relatively poorer Trichalinina fauna there. Australia has in fact impoverished Papuan fauna. Most representatives occur in the northeastern part where humid tropical forests occur. It is supposed that New Guinea had been connected with Australia since Miocene and the lost of connection is quite recent. This fact can explain the distribution of Trichalinina in Australia. The youth of Torres strait decrease its value as a vicariance border when evaluating genera and only specific endemits are encountered on both sides of the strait. Only one species is recorded from both sides of Torres straight: *Trichalus acutangulus* Waterhouse, 1878 is known from New Guinea and Queensland, all remaining species are endemits of either Australia or New Guinea. In the case of this geologically measured temporary water barrier it is necessary to point out that this area can be an effective vicariance barrier even if dried and forested. Most species of Trichalinina are endemic to mountain forest on isolated mountains but south of New Guinea and northernmost Australia do not have higher mountains and are mainly covered by eucalyptus forests or mangrove in swamps. Such habitats can serve as barrier for lycids occurring in mountains very effectively, because of their low vagility.

The same very low specific similarity has been found between fauna of individual islands of the Great Sundas and such situation is generally very common in Lycidae. I explain this fact by very low vagility of Lycidae living in lower strata of humid forests resulting in effective isolation of smaller populations and subsequent speciation. This isolation effect of lowland forests is similar to that of the Torres strait area. The future study of this group on the species level can bring more accurate information for understanding of its biogeography.

The described distribution of newly restricted Trichalinina supports the hypothesis (discussed in the chapter about phylogeny) that they are very young group which underwent speciation during the formation of island area between Asia and Australia It can be supposed that they evolved in Papuan subregion or both Papuan and Moluccan subregions and this area has been increased by migration to the south to Australia and to the north to the Philippines and Indochina

The clade *Leptotrichalus* + *Lobatang* has the center of distribution in the archipelago between Australia and Asia No species has been found either in Pacific islands north and east of New Guinea or in Australia The genus *Lobatang* includes four species, three of them are known from New Guinea, one from southern Sulawesi All known species were collected in elevations around 1000 m a s l Ranges of these genera overlap each other in Sulawesi only Much more specious genus *Leptotrichalus* is distributed on the Philippines (29 species), Borneo (7), Sumatra, Peninsular Malaysia (2), Indochina (1), Java (9) Celebes (4) and Lesser Sundas (1) The origin of this group in the archipelago not on the mainland is supported by the rarely encountered fact that Java houses more species than Sumatra The comparison of the distribution of mimicry complexes is very interesting in case of *Leptotrichalus* Lycids are slightly poisonous and they very often serve as models in numerous mimicry complexes Any striking difference has not been found between fauna of the island chain of Java and the Lesser Sundas, except relative species poverty of small islands All species known from islands on both sides of Wallace's line are completely yellow or yellow with an apical part of elytra black The species distributed on Sulawesi and the Philippines belong to the same complex The range of distribution of this complex is in congruence with the zoogeographic border as defined by Wallace in its middle part between Borneo and Sulawesi, to the north it agrees with Huxley's line A more discriminating picture of the distribution of mimicry complexes of *Leptotrichalus* may be gained when comparing the distribution of this genus to the ratio of dry and wet months of year The common characteristic of all islands where yellow *Leptotrichalus* occurs is regular long dry season The *Leptotrichalus* species known from Sumatra, Borneo, Peninsular Malaysia and Indochina are often mostly black or brown but never yellow The area where they occur is much more humid during whole year

The representatives of the clade *Diatrichalus* + *Enylus* are widespread *Diatrichalus* is known in the north from the Philippines, Malaysia, Sumatra and Borneo, to the south it reaches Australia The highest species richness has been found in New Guinea, from where nearly one hundred species are deposited in the collections of SMNS and MNHH and will be described in future paper *Diatrichalus* is known also from Solomon island The distribution of this genus agrees nearly completely with distribution of *Microtrichalus* and its origin in eastern Malesia and subsequent speciation can be supposed also in this case *Enylus* is much less specious and it occurs in New Guinea and Australia only

The genus *Kassemia* gen n is endemic to New Guinea According to the phylogenetic analysis it is much less related to the Trichalinina than to other Metriorrhynchini genera and its position and zoogeographic history can be elucidated only after analysis of the whole subfamily

TAXONOMY

Review of Metriorrhynchini with the shortened first elytral primary costa

Trichalinae were introduced to the classification of Lycidae as the subfamily and regardless later lowering to the tribe rank they were whole time considered by Kleine to be coordinate taxon to all other subfamilies or tribes in Lycidae This view was not followed by Bocák & Bocaková (1990) and Trichalini were lowered to the subtribe rank within the tribe Metriorrhynchini but also in this paper they were considered to be a monophyletic group based on one presumably shared advanced character–shortened first primary elytral costa and basal position of this clade was supported also by the presence of primitive pattern of the pronotal carinae arrangement in genera *Schizotrichalus* and *Enclases* which were supposed to be more primitive than genera *Diatrichalus* and *Leptotrichalus* The shortened first primary elytral costa was useful for practical identification, but it was not proved in the present analysis, that it is unique apomorphy Only the clade *Flabellotrichalus* + *Trichalus* + *Microtrichalus* + *Schizotrichalus* + *Enclases* (see cladogram) is included to the subtribe Trichalinina here, the remaining former genera of Trichalinina (*Diatrichalus* and *Leptotrichalus*) are classified incertae sedis within Metriorrhynchini The whole tribe Metriorrhynchini, which now includes 46 described genera and some dozens of not yet described in available material, needs badly a complete taxonomical revision based on the reliable phylogenetic analysis

Metriorrhynchini Kleine, 1926

Trichalinina Kleine, 1928

Trichalinae Kleine 1928 222
Trichalini Kleine 1933 69
Trichalinina Bocak et Bocaková, 1990 646 (type-genus *Trichalus* C O Waterhouse 1877 82)

DIAGNOSIS First primary elytral costa shortened, pronotum with one areola in most representatives (Fig 35), sometimes five areolae (Fig 36) or two divergent ridges (Fig 39) present Male genitalia slender, internal sac exposed, membranous (Figs 56–59). Vagina with two dorsally attached glands (Figs 68–70)

REDESCRIPTION Body small to medium sized (4–20 mm), dorsoventrally flattened, elytra parallel-sided or more or less widened backwards, variable in coloration, often with aposematic color patterns

Head hypognathous, small, partly hidden by pronotum, rostrum absent Cranium slightly dorsoventrally flattened, without sutures, only gular suture sometimes partly present, with more or less prominent antennal tubercles followed by depression on the upper surface of cranium, mouth opening approximately as wide as long, in frontolateral part emarginate Gula wider than long, with more or less wide process, where postmentum is attached, posterior tentorial pits usually unapparent externally, tentorium mostly membranous, only posterior tentorial arm partly sclerotized Mandibles relatively stout, short, curved in apical part in right angle, inner margin without dents, outer margin covered with dense long setae, sometimes only several short pale setae present Labrum wider than long, sometimes with shallow emargination at frontal margin, which bears long dense setae Epipharynx attached to the labrum in basal part through two well sclerotized arms identical with the same in *Diatrichalus*, or sometimes these arms shorter, closely attached to the bottom surface of lateral margins of labrum Labium with robust praementum and much smaller U-shaped postmentum Labial palpi with three palpomeres, palpomere 2 usually the longest one Hypopharynx flat, with lateral margins more sclerotized and partly bent, firmly connected with bottom part of praementum through frontal processes Maxillae with apparent long galea, lacinia smaller, sometimes reduced to limited field of pale shorter setae Cardo very small, well sclerotized, movable, stipes flat, usually with narrow bent inner margin Maxillary palpi with four palpomeres, palpomeres 1 and 3 always much smaller than palpomeres 2 and 4 Apical palpomeres flattened in distally Antennae with 11 antennomeres, slightly to very strongly flattened, usually serrate in both sexes or lamellate in male and serrate in female Antennomere 1 pear-shaped, robust, antennomere 2 very small, short, both proximal antennomeres never flattened in contrast with all following distal antennomeres Antennomeres 3–10 serrate in various degree, antennomere 11 elliptic Whole surface of antennomere 3–11 covered with dense, short pubescence In membrane between head and pronotum two cervical sclerites present laterally

Prothorax with flat shield-form pronotum bearing ridges In most species (genera *Trichalus Microtrichalus* and *Flabellotrichalus*) two longitudinal carinae forming lanceolate central areola present only or two divergent longitudinal carinae form V-shape pattern (genus *Enicl**ases*) or three areolae are present within the area limited by longitudinal carinae (genus *Schizotrichalus*) If central areola present, then either connected with frontal margin by carina or adjacent directly to the margin, length of connecting carina variable Sometimes strengthened keels present in posterior part of lateral margins, these keels present in most species of subtribe irregularly, in this position there is also more or less apparent dent At frontal and lateral margins surface of pronotum punctured Pubescence of pronotum usually short, not very dense in most species, much denser at lateral margins in most *Flabellotrichalus*, sometimes very long and apparent Pleural part of prothorax dish-like, with strongly elevated margins, always with the same structure of surface as pronotum Prothoracal coxae open, prothoracal trochantin with slim process, uniform within Metriorrhynchini, mesosternum transverse, narrow, bridge-like Basisternum trapezoidal, more or less convex, with two divergent processes attached to apical part Mesothorax relatively small, firmly fused with metathorax, mesosternum triangular, much wider than long, moderately emarginate at frontal margin, more or less widely connected with metasternum Mesepisternum with distal process reaching to mesocoxal cavity Mesonotum small, only distal part of mesoscutellum visible in upper view, apex of mesoscutellum moderately emarginate Metathorax long, robust, metasternum broad and long, with incomplete midline in distal part, slightly emarginate between metacoxae, metanotum flat, alacristae occupying apparently less than half of metanotal length, scutoscutellar sutures slightly curved, long, reaching distal margin of metanotum, metascutellum often slightly emarginate, and sometimes with apparent longitudinal keel Postnotum transverse, with bent distal margin and often with longitudinal keel Elytra flat, parallel-sided or slightly widened backwards, with nine longitudinal costae on each elytron in Trichalinina at base of elytron only Four costae (costa 2, 4, 6 and 8) much stronger than remaining ones are called primary costae Primary costa 1 strong only in first quarter of elytron, then primary costa 1 much weaker, as strong as secondary costae Secondary costae between suture and primary costa 1 and between primary costae 1 and 2 missing except humeral quarter of elytron Wing venation uniform within subfamily Metriorrhynchinae and identical with most representatives of other subfamilies of Lycidae

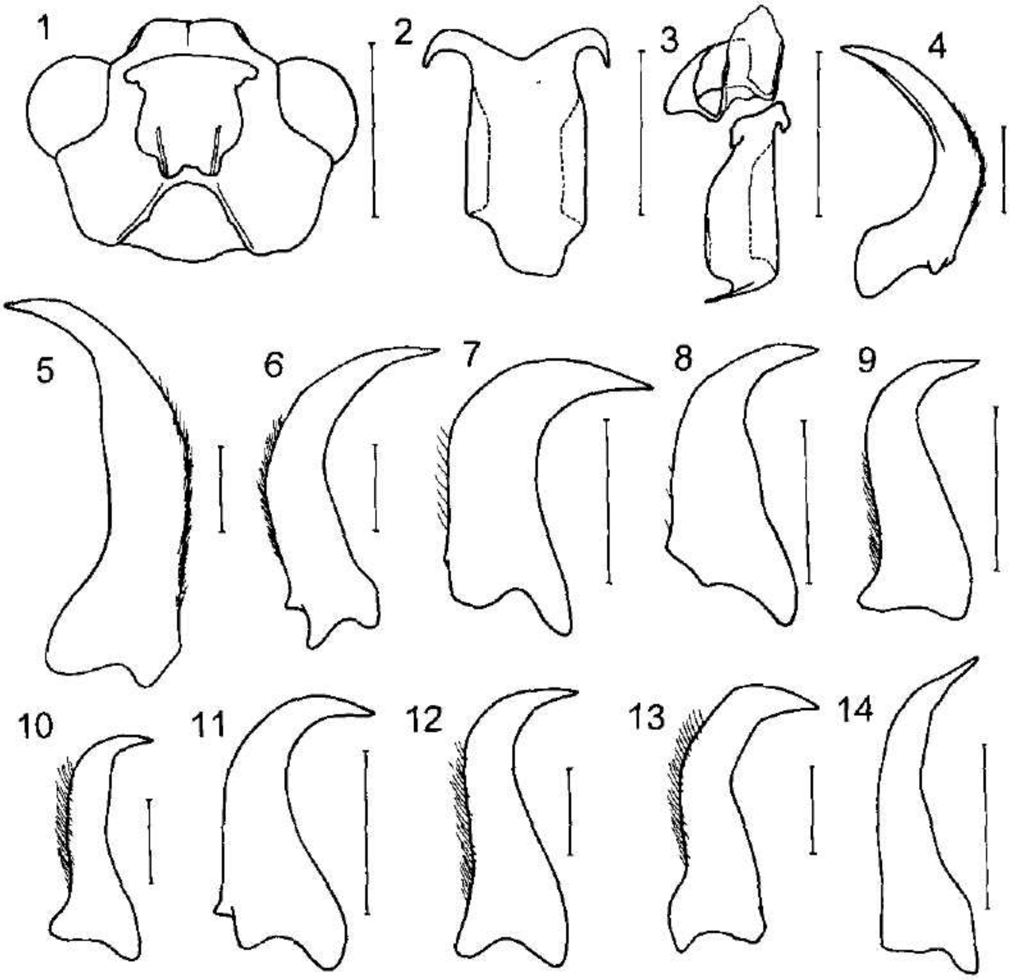
Abdomen with eight visible segments in male and seven in female, flat, all segments freely movable, no connotation of segments present, eight functional abdominal spiracles present, first much bigger, closely adjacent to hind margin of postnotum, others small but open, situated in connecting membrane, their position stable within subfamily

Shape of two male terminal sternites influenced by the shape of male genitalia, often slender, highly convex, enrolling the phallus Subapical male abdominal sternite always more or less emarginate at hind margin Last visible tergite long, spoon-like, often with small sclerotized segment attached to the inner surface, this tergite sometimes membranous, undetectable

Female last visible sternite with very short, lightly sclerotized or missing spiculum gastrale, often apparently emarginate at apical margin

Male genitalia uniform in high degree within subtribe Phallobase annuliform, subtle, with more or less extensive membrane over opening, but membrane is always soft, not sclerotized and keeping some form (compare with *Leptotrichalus* with member of Trichalinina) Paramerae missing, phallus always slender, with well sclerotized apical part, open ventrally with exposed internal sac Internal sac membranous, often with pair of slender sickle-like thorns at base, only sometimes with subtle V-shaped rod in membrane

Ovipositor with usually long, slender valvifers, sometimes connected at their base by membrane, which can be sclerotized in high degree, than valvifers basally fused Valvifers in *Trichalus* robust, connected in basal third. Vagina often slender, longer than valvifers, accessory lateral gland inserted dorsally. Bases of glandular ducts sometimes more robust (*Trichalus*), usually slender but more sclerotized than proper gland, special lateral pockets of unknown function found in *Microtrichalus*. In all genera flat unpaired gland present in apical part of vagina, additional extremely slender unpaired basal gland has been found in *Microtrichalus*. Spermatheca lemon-like, with short to



Figs 1–14. 1 – head ventrally, *Diatrichalus* sp., 2 – hypopharynx of *Diatrichalus* sp., 3 – labrum, hypopharynx and epipharynx of *Diatrichalus* sp, ventrolateral view, 4–14. Mandible: 4 – *Kassemia oculata* sp n., 5 – *Metriorrhynchus parallelus* (Guérin Méneville), 6 – *Lobatang papuensis* sp. n, 7 – *Diatrichalus xylobanoides* Kleine, 8 – *Schizotrichalus* sp, 9 – *Microtrichalus basipennis* (Pic), 10 – *Enclases luteolus* Waterhouse, 11 – *Enylus* sp, 12 – *Trichalus flavopictus* Waterhouse, 13 – *Flabellotrichalus flabellatus* (Bourgeois), 14 – *Leptotrichalus cyaniventris* (Kirsch) Scales 0 5 mm.

moderately long, in most cases curved spermaduct. Spermathecal gland attached to apex of spermatheca.

SEXUAL DIMORPHISM. Females only very slightly bigger, males of most species with much larger eyes, size of female eyes smaller and uniform within groups of related species. Male antennae often more acutely serrate than female ones. Only in three species of *Eniclases* and in genus *Flabellotrichalus* males with flabellate and females with serrate antennae.

DISTRIBUTION. The subtribe Trichalinina is a pure Austro-Oriental group with the highest diversity both in species and genera in Papuan subregion. Northern limit of range lies in central Vietnam, Laos and Thailand and in Burmese Tenasserim, from where only several species are known at present. Easternmost records originate from the Philippines which accommodate several species of *Microtrichalus* and from the Solomon Islands. They have not been recorded from French Polynesia or New Zealand. Many species are known from Australia including Tasmania.

***Trichalus* C. O. Waterhouse, 1877**

(Figs 12, 15, 25, 44, 46–47, 49, 64, 68)

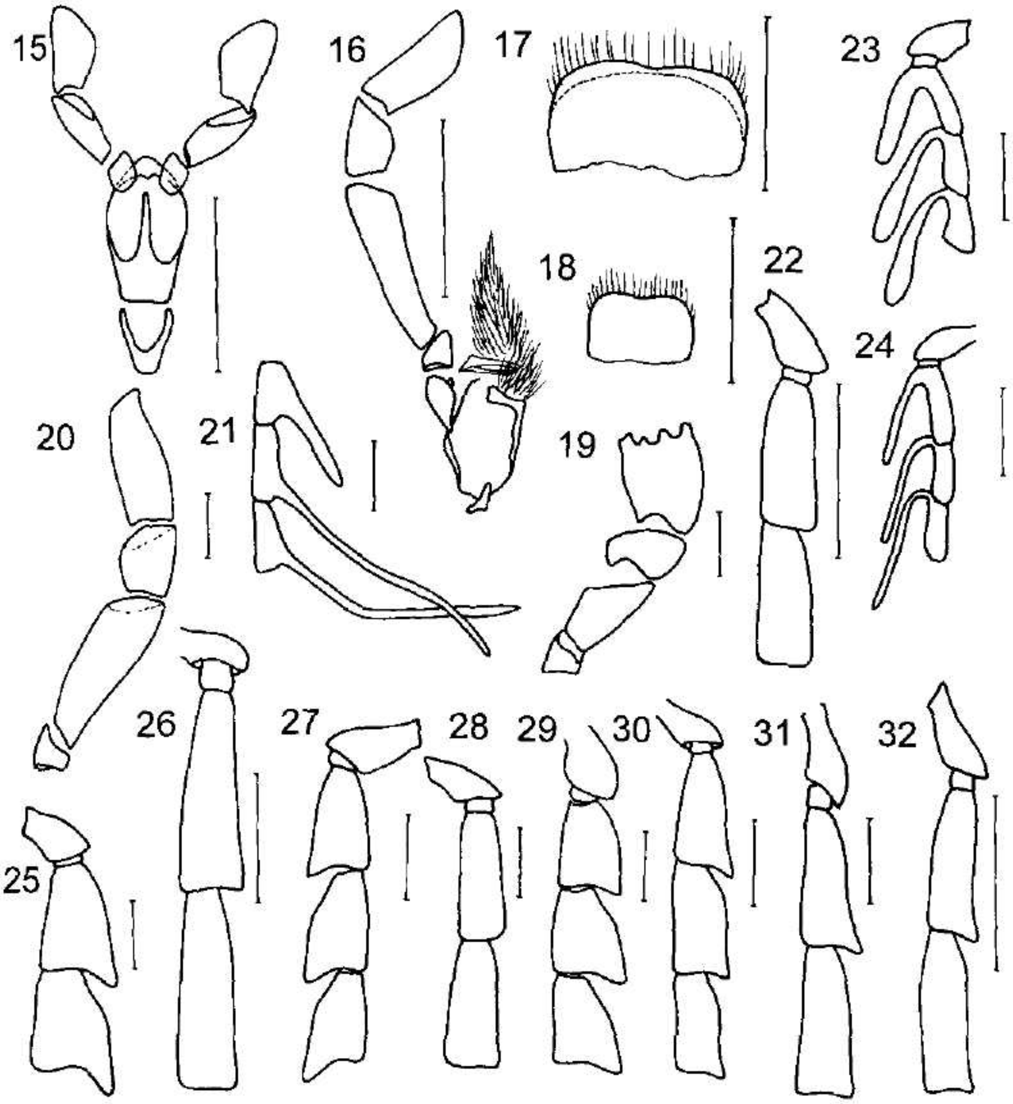
Trichalus Waterhouse, 1877. 82 (type species, *T flavopictus* Waterhouse, 1877, Waterhouse 1878 103)
Xantheros Fairmaire 1877 167, Fairmaire 1879 99 (type species *X ochreatus* Fairmaire, 1877, Bourgeois 1891 347)

DIAGNOSIS. Antennae serrate in male, pronotum with one longitudinal median areola, first elytral primary costa shortened, male genitalia with two thorns at base of internal sac. Lateral glands attached dorsally, valvifers connected subbasally, forming H-shaped figure (Fig. 64), apical maxillar palpomere much broader than in *Microtrichalus*, bases of coxae with short process (Fig. 49).

REDESCRIPTION. Body medium sized, dorso-ventrally flattened, parallel-sided to slightly widened backwards.

Head small, hypognathous, partly concealed by pronotum, antennal tubercles prominent, followed by shallow transversal depression behind them, eyes large, gular sutures unapparent, distance between posterior tentorial pits larger than length of gula, posterior tentorial arms, short, moderately sclerotized, clypeus wide, concave, mandibles robust, nearly twice longer than clypeus, inner margin twice weakly broken, in apical half with very fine small dents, apical part curved in right angle, outer margin with dense pubescence. Labrum wider than long, with lateral arm connected with epipharynx. Epipharynx membranous, with tiny setae, deeply emarginate at apex, hypopharynx concave in apical part, bent lateral parts only very narrow. Labium with robust praementum, postmentum quite well developed, V-shaped, with long arms. Labial palpi quite robust, moderately compressed, apical palpomere nearly parallel-sided. Maxillae with very tiny cardo, plate-like, large stipes, long well developed galea and much smaller lacinia. Maxillary palpi with palpomere 2 largest of all, apical palpomere broad, obliquely cut at apex. Pronotum broad, broader than long, with one longitudinal quite broad areola in middle, lateral margins elevated, convex. Basisternum robust, trapezoidal, strongly convex, with longitudinal keel, apical processes long, slender. Mesosternum attached to metasternum through narrow keel, frontal part of mesosternum nearly straight. Mesoscutellum widely emarginate. Metasternal midline apparent, occupying nine tenth of metasternal length. Both metascutellum and postnotum weakly emarginate at hind margin and with longitudinal keel. Elytra slightly widened backwards, with first primary costa shortened, secondary costae always well developed, regular. Legs strongly compressed, moderately long, quite robust. Hind coxa with process near attachment of trochanter, covered with dense pubescence, hind trochanter globuliform, short.

Male genitalia with slender phallus, internal sac membranous, with pair of dents at base, internal sac exposed, free, phallobase annuliform. Ovipositor with extremely robust valvifers, fused in basal



Figs 15–32. 15 – Labium of *Trichalus flavopictus* Waterhouse, 16 – Maxilla of *Eniclases luteolus* Waterhouse, 17 – labrum of *E. luteolus* Waterhouse, dorsal view, 18 – dtto of *Diatrichalus* sp., 19 – maxillary palpus of *Diatrichalus* sp., 20 – dtto of *Microtrichalus basipennis* (Pic), 21 – male antennomeres 3–5 of *Flabellotrichalus novaeguineensis* Bocák, 22 – female basal antennomeres of *Lobatang miserandus* (Kleine), 23–32: Male basal antennomeres: 23 – *Kassemia oculata* sp. n., 24 – *K. sedlacekiae* sp. n., 25 – *Trichalus flavopictus* Waterhouse, 26 – *Lobatang sordescens* (Bourgeois), 27 – *Schizotrichalus* sp., 28 – *Leptotrichalus cyaniventris* (Kirsch), 29 – *Eniylus amplus* Kleine, 30 – *Diatrichalus xylobanoides* Kleine, 31 – *Microtrichalus* sp., 32 – *Lobatang acuticornis* sp. n. Scales for 15–18 and 21–32 0.5 mm, scales for 19–20 0.1 mm.

third, flat, attached to coxital processes. Vagina robust, lateral accessory glands attached dorsally, their bases widened, unpaired vaginal gland short, present, spermathecal duct short, only slightly curved, spermatheca large, with Y-shaped gland.

Distribution. The representatives of the genus *Trichalus* have been found in Australia only. Although most species of Trichalinina were previously described in this genus, the species, whose holotypes or lectotypes were studied, should be transferred in prepared alpha-taxonomical revisions to the genera *Diatrichalus* and *Microtrichalus*. Many species occurring in other regions have not yet been studied and they are classified provisionally with *Trichalus* (status quo is kept at present).

Remarks. It has been believed that the genus *Xantheros* was described by Fairmaire (1879) but this genus is diagnosed and named already by Fairmaire (1877). Exact data of publication are given in both publications where *Trichalus* and *Xantheros* were described and according to them the genus *Xantheros* is a junior subjective synonym of *Trichalus*. Fairmaire (1877) classified three Australian species within *Xantheros* and subsequently *X. ochreatus* was designated as a type species by Bourgeois, 1891. The type of *Xantheros ochreatus* has not been studied. It should be deposited in the Hamburg Museum, but substantial part of collections of this museum was destroyed during World War II and the type of this species was not found. Therefore, long time kept synonymical status of *Xantheros* is followed here.

Microtrichalus Pic, 1921

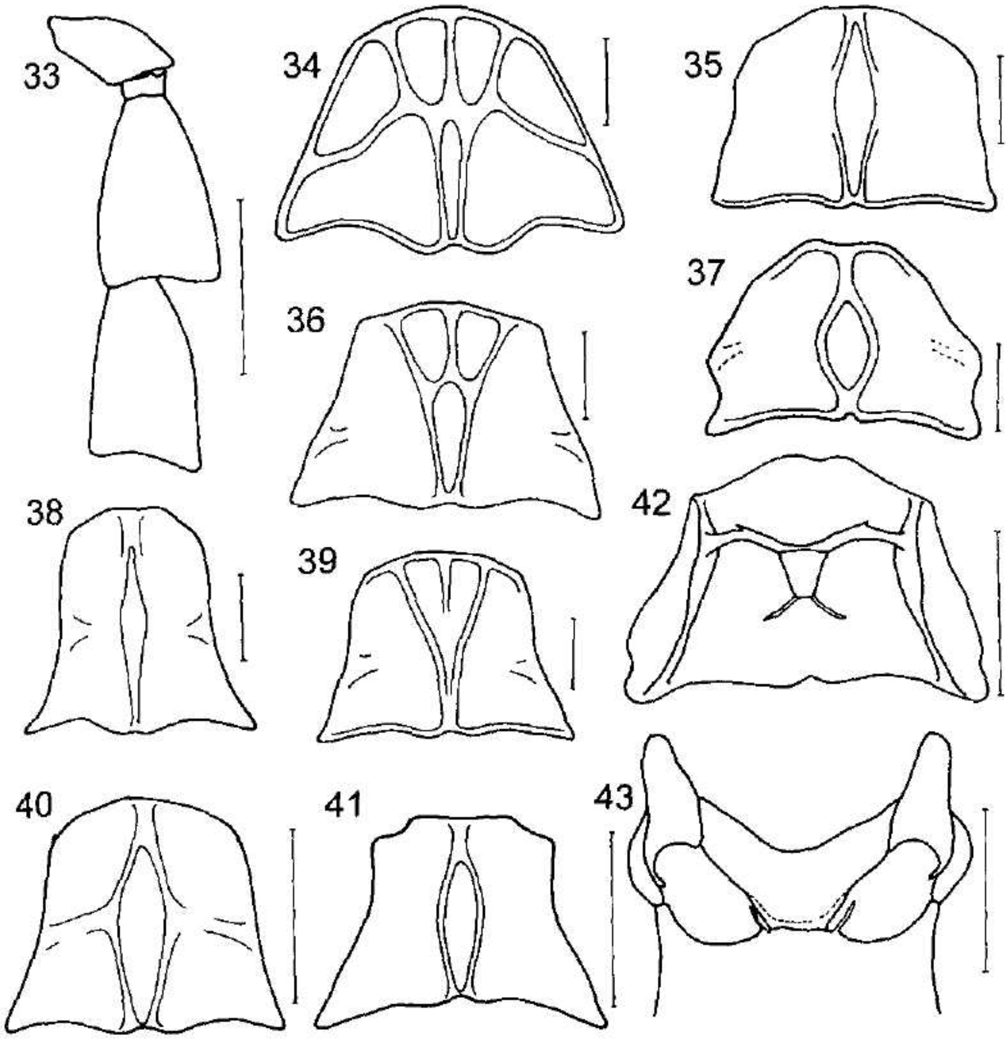
(Figs 9, 20, 31, 59, 69)

Microtrichalus Pic, 1921: 9, hors texte (type species *M. singularis* Pic, 1921, by monotypy)
Falsoenylus Pic, 1926: 29, hors texte – **syn. n.** (type species. *F. basipennis* Pic, 1926, by monotypy)
Microtrichalus basipennis (Pic, 1926) – **comb. n.**

Diagnosis. Antennae serrate in male, pronotum with one longitudinal median areola, first elytral primary costa shortened, male genitalia with two thorns at base of internal sac and narrowed apical part of phallus. Lateral glands attached dorsally, vagina with two lateral pockets (Fig. 69) situated in the middle of vaginal length, one very slim and long unpaired gland between valvifers (Fig. 69), valvifers slender, sometimes fused basally.

Redescription. Body small to medium sized, dorso-ventrally flattened, parallel-sided to slightly widened backwards, generally less sclerotized. Very often with dorsal part of body at least partly yellow to light brown.

Head small, concealed by pronotum, hypognathous, gula shorter than distance between tentorial pits, gular sutures unapparent, posterior tentorial arms well sclerotized. Eyes hemispherically prominent, large, usually much larger in males. Antennal tubercles present, moderately prominent. Mandibles moderately stout, inner margin slightly twice broken in apical part, apex curved in right angle. Labrum wider than long, only very weakly emarginate at apex, with lateral arms well sclerotized, hypopharynx with wide bent lateral margins. Praementum stout, postmentum well developed, V-shaped, with long arms, quite robust. Labial palpi slender, apical palpomere slightly narrowed to apex, compressed. Maxillae with very small cardo and relatively large plate-like stipes, galea long, densely setose, lacinia much smaller, maxillary palpi slender, apical palpomere nearly parallel-sided, slightly narrowed to apex, compressed, palpomere 2 longest. Antennae always strongly compressed from antennomere 3 to 11, densely pubescent, antennomeres 3–10 parallel-sided to serrate, never flabellate. Pronotum always widest at base, usually with apparent dents at basal third of lateral margins, narrow to moderately broad longitudinal areola in middle. Frontal margin of proepisternum nearly straight, basisternum trapezoidal, with slender apical processes. Attachment of mesosternum to metasternum narrow, frontal margin of mesosternum slightly concave. Mesoscutellum emarginate at apex. Hind margin of metascutellum deeply emarginate and with longitudinal keel in midline dividing metascutellum nearly completely, hind margin of postnotum bilobed, with longitudinal keel. Elytra flat, primary costa 1 shortened, secondary costae always present, only in some



Figs 33–43. 33 – male basal antennomeres of *Lobatang papuensis* sp. n., Figs 34–41. Pronotum. 34 – *Metriorrhynchus flavicostatus* Kleine, 35 – *Enylus amplus* Kleine, 36 – *Schizotrichalus nigrescens* Waterhouse, 37 – *Diatrichalus absonus* (Kleine), 38 – *Leptotrichalus accuratus* Kleine, 39 – *Eniclases moluccanus* Kleine, 40 – *Lobatang miserandus* (Kleine), 41 – *L. acuticornis* sp. n., 42 – prosternum of *Diatrichalus xylobanoides* Kleine, 43 – mesosternum of *Schizotrichalus* sp. Scales 0.5 mm.

species rarely irregularly interrupted. Legs always strongly compressed, usually very slender. Abdomen narrower than elytra, movable, flat.

Male genitalia very uniform within genus. Phallobase ring-like, never with sclerotized membrane, phallus slender, only in basal part sclerotized ventrally and dorsally, in apical part open ventrally, internal sac exposed, with pair of sickle-like thorns at base, sometimes with V-shaped rod in membrane. Whole male genitalia often very slightly pigmented and sclerotized, then structure of internal sac unapparent. Ovipositor with slender, sometimes fused valvifers. Vagina slender to moderately robust, with dorsally attached lateral accessory glands whose bases are more sclerotized, proper gland is very fine. Two lateral pockets of unknown function are present in lateral part of vagina. Very slender unpaired gland attached to base of vagina. Spermatheca lemon-like, spermaduct more or less curved.

DISTRIBUTION. The genus is widely distributed in the Oriental Region. Some Australian species until now classified with *Trichalus* are known from northern Queensland. The exact extent of the range of *Microtrichalus* in Australia is not known at present.

REMARK. Holotype of type species *Microtrichalus singularis* was studied and it was found to be congeneric with *Falsoenylus basipennis* and therefore *Falsoenylus* is here considered to be a junior subjective synonym of *Microtrichalus*.

***Flabellotrichalus* Pic, 1921**

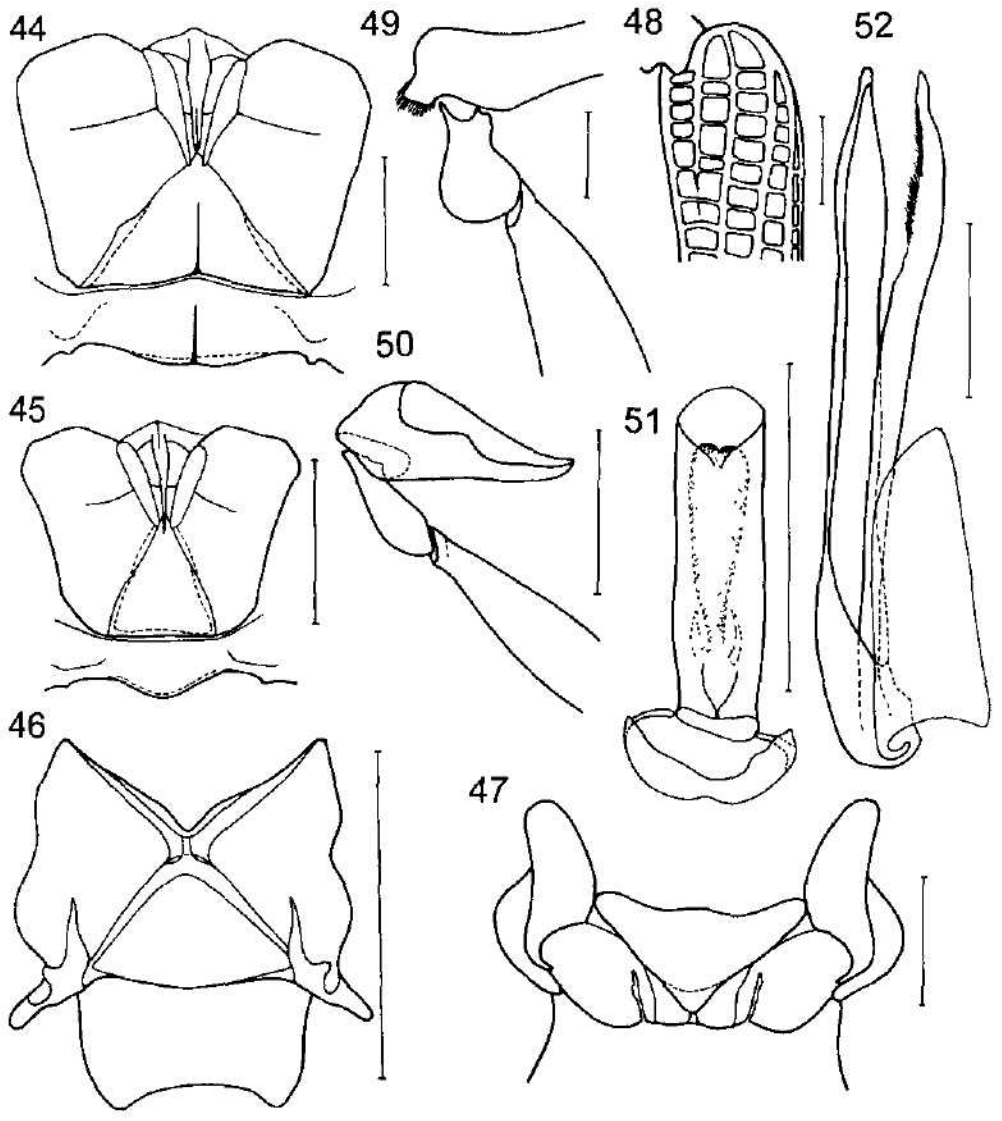
(Figs 13, 21, 58)

Flabellotrichalus Pic, 1921: 9, hors texte (type species *F. notatithorax* Pic, 1921, subsequently designated by Kleine (1936: 4)).
Stereotrichalus Kleine, 1926: 183 (type species *S. evidens* Kleine, 1926: Kleine 1930).
Villosotrichalus Pic, 1921: 9, hors texte, **syn. n.** (type species *V. reductus* Pic, 1921, by monotypy).

DIAGNOSIS. Antennae flabellate in male (Fig. 21), pronotum with one longitudinal median areola, frontal and lateral margins of pronotum very often with dense short to very long pubescence, first elytral primary costa shortened, male genitalia without any thorns at base of internal sac. Male genitalia very slender, whole internal sac always membranous. Lateral glands of vagina attached dorsally.

REDESCRIPTION. Body medium sized to large, dorsoventrally flattened, slightly widened backwards. Usually dark brown to black with humeral part of elytra lighter.

Head small, hypognathous, partly concealed by pronotum, antennal tubercles moderately prominent, followed by very shallow transversal depression behind them. Eyes large. Gula wide and short, much shorter than distance between posterior tentorial pits, hind margin of gula very concave, frontal margin projected in narrowed process. Clypeus slightly emarginate in middle, bilobed, labrum wider than long, with lateral arms apparent but closely connected with lateral margins of pronotum in their whole length, frontal margin slightly emarginate, epipharynx unpigmented, very fine, hypopharynx membranous in distal part, with slender lateral processes, praementum well developed, robust, firmly connected with hypopharynx, postmentum very reduced of irregular shape. Labial palpi slender, with apical palpomere strongly compressed, slightly narrowed at apex. Maxillae with very small cardo, plate-like stipes, galea robust, lacinia very small. Mandibles stout, much longer than labrum, inner margin twice broken in apical part, apex slender, curved in right angle. Antennae flabellate in male (antennomeres 3–10), strongly compressed, serrate in female, length of lamellae different in various species. Pronotum flat, with one longitudinal areola in middle, often with more or less dense and long pubescence at lateral margins. Proepisternum slender, its frontal margin concave, basisternum trapezoidal, with very slender apical processes. Mesoscutellum emarginate at apex, with long lateral processes. Mesosternal frontal margin slightly concave, mesosternum attached to metasternum in short line. Metascutellum without keel, postnotum bilobed at hind margin, with keel. Elytra flat, primary costa 1 shortened, secondary costae always present. Legs moderately slender, strongly compressed. Abdomen slender, flat.



Figs 44–52. 44–45. Metanotum: 44 –*Trichalus flavopictus* Waterhouse, 45 – *Schizotrichalus* sp., 46 – scutellum of *Trichalus flavopictus* Waterhouse, 47 – mesosternum of *Trichalus flavopictus* Waterhouse, 48 – Humeral part of elytron of *Kassemia sedlacekiae* sp. n., 49 – 50: Hind coxae, trochanters and bases of femora. 49 – *Trichalus flavopictus* Waterhouse, 50 – *Schizotrichalus* sp., 51–52: Male genitalia: 51 – *Kassemia sedlacekiae* sp. n., 52 – *Lobatang acuticornis* sp. n. Scales 0.5 mm.

Male genitalia very slender, phallobase ring-like, sometimes covered with extensive membrane. Phallus very long, narrow, sclerotized completely only in basal part, in apical portion sclerotized only dorsally, internal sac exposed, pigmented at apex, sometimes with strengthened rod in membrane, never with pair of thorns at base. Ovipositor with slender valvifers. Vagina with two dorsally attached accessory glands, glands very fine, bases of glandular ducts much stronger, unpaired flat gland quite long, spermaduct long, curved, spermatheca lemon-like.

Distribution. The representatives of *Flabellotrichalus* are known only from New Guinea and its adjacent islands and from the Moluccas. I have checked the types of the Flabellotrichalus representatives recorded from the Solomon Islands and they belong in fact to the genus *Diatrichalus* Their taxonomical position will be discussed in another paper. Three species were described from Australia by Lea (1909) and Kleine (1930); the identity of these species has not been checked yet.

Eniclases C. O. Waterhouse, 1879

(Figs 10, 16–17, 39, 56, 70)

Eniclases Waterhouse, 1879 66, Waterhouse (1878: 103) (type species: *Lycus* (genus 35) *luteolus* Waterhouse, 1878 (by original designation)

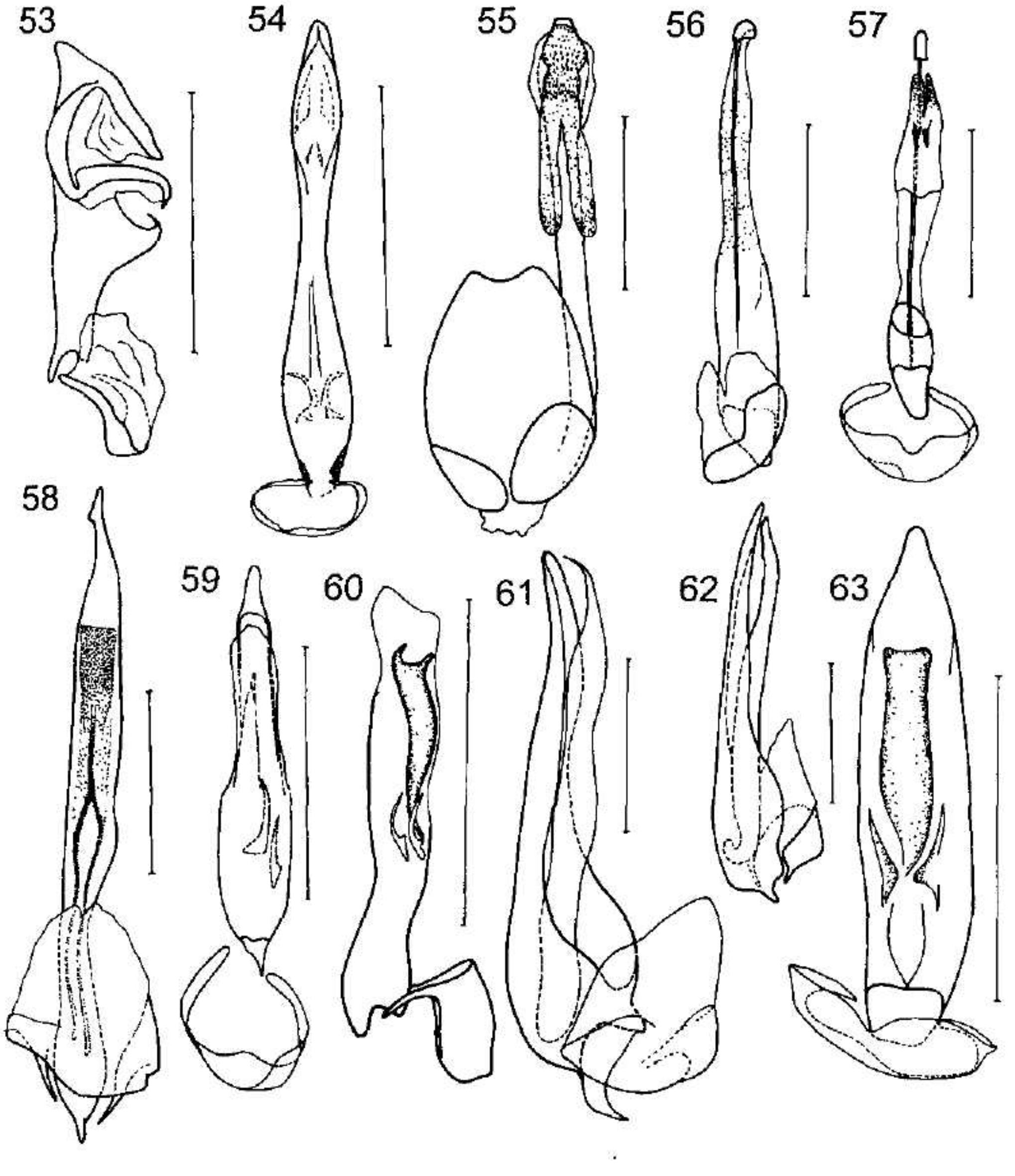
Trichalolus Pic, 1923: 36, hors texte; Bocák & Bocáková (1991 206) (type species. *T. apertus* Pic, 1923, by monotypy).

Diagnosis. Pronotum with two longitudinal divergent carinae dividing pronotum in three fields (Fig. 39), first elytral primary costa shortened, male genitalia without any thorns at base of internal sac. Male genitalia very slender, whole internal sac always membranous, phallus with darkened strengthened keel (Fig. 56). Lateral glands of vagina attached dorsally (Fig. 70).

Redescription. Body medium sized to moderately large (6.8–17.5 mm), slender to moderately robust, parallel-sided to slightly widened backwards, many species with light yellow dorsal side, but some completely dark brown to black or dark brown with lighter pronotum or pronotum and basal part of elytra.

Head small, partly hidden by pronotum, male eye diameter usually bigger than distance of eyes (1.1 to 1.4 in most species), only rarely smaller (*E. flabellatus* Bocák et Bocáková, 1991). Gula approximately as long as wide, gular sutures unapparent, posterior tentorial arm short, but well sclerotized. Labrum slightly emarginate in apical part, with long lateral arms. Epipharynx large, deeply emarginate at apex, fully membranous. Hypopharynx flat, with bent lateral margins. Mandibles quite long, not very robust, with flat dent in apical third. Labium with robust praementum and U-shaped, moderately robust postmentum Labial palpi slender, with parallel-sided apical palpomere. Maxilla with small cardo (one tenth of stipes length), galea reduced but present, lacinia moderately long. Maxillary palpi slender, apical palpomere nearly parallel-sided. Antennae with parallel-sided to serrate antennomeres 3–10, only in several species antennomeres flabellate in male. Pronotum small, usually narrower than humeri of elytra, always widest at base; two divergent longitudinal carinae present on the pronotum, more or less strong short carina in frontal part of midline often present, lateral margins with obtuse dent in basal third. Elytra with shortened primary costa 1, flat, with complete secondary costae. Both male and female genitalia uniform in high extent within whole genus. Male genitalia with apparent keel in dorsal side of phallus, with free internal sac, usually membranous, without any special structures or thorns, only in *Eniclases riedeli* Bocák, 1997 more sclerotized, never with sclerotized membrane of phallobase. Ovipositor with basal processes of coxae attached to valvifers, lateral glands of vagina attached in middle part of vagina, bases of glandular ducts sclerotized, glands very fine (Fig. 70). Spiculum gastrale very short. Legs very slender to moderately robust, strongly compressed.

DISTRIBUTION. At present, 25 species are known from New Guinea and one species from the Moluccas. Despite of the very extensive material from the Solomon islands no species has been recorded there.



Figs 53–63. Male genitalia: 53 – *Diatrichalus* sp., 54 – *Enylus segregatus* Waterhouse, 55 – *Leptotrichalus accuratus* Kleine, 56 – *Eniclases electus* Kleine, 57 – *Schizotrichalus nigrescens* (Waterhouse), 58 – *Flabellotrichalus notatithorax* (Pic), 59 – *Microtrichalus basipennis* (Pic), 60 – *Kassemia wauensis* sp. n., 61 – *Lobatang papuensis* sp. n., 62 – *L. sordescens* (Bourgeois), 63 – *Kassemia oculata* sp. n. Scales 0.5 mm.

Schizotrichalus Kleine, 1926
(Figs 8, 27, 36, 43, 45, 50, 57)

Schizotrichalus Kleine, 1926: 167 (type species: *T. nigrescens* Waterhouse, 1879, by original designation).

Diagnosis. Pronotum with five areolae (Fig. 36), first elytral primary costa shortened, male genitalia without any thorns at base of internal sac, phallus with darkened strengthened keel (Fig. 57). Lateral glands of vagina attached dorsally.

Redescription. Body small to medium sized, flattened dorsoventrally, elytra slightly widened backwards, dark brown to black, one species with humeri and lateral parts of each elytron light brown.

Head small, partly concealed by pronotum, hypognathous, eyes large, antennal tubercles less prominent. Gula much wider than long, transverse, gular sutures missing. Labrum wider than long, very slightly emarginate at apex, with well developed lateral arms and bent lateral margins, hypopharynx less sclerotized, mandibles quite robust, inner margin twice broken, apex slender, sharp. Labium with robust praementum and well developed approximately as long as wide postmentum, labial palpi slender, apical palpomere narrowed at apex, flattened. Maxillae with small cardo, large stipes, long galea and reduced lacinia. Maxillary palpi slender, palpomere 2 longest. Antennae strongly compressed, moderately serrate, without apparent sexual dimorphism. Pronotum with five areolae, slightly broader than wide. Basisternum trapezoidal, with much less apparent longitudinal keel than in related genera. Mesosternum widely attached to metasternum, frontal margin strongly concave. Mesoscutum slightly emarginate at apex, metascutellum without longitudinal keel, distal margin bent. Elytra with first costa shortened, mostly all secondary costae developed, in one (presently undescribed) species irregular transverse costae and mostly missing secondary costae were found. Abdomen slender, narrower than elytra. Legs strongly compressed, moderately long.

Male genitalia with long, slender, only in basal part well sclerotized phallus, dorsal part with one strengthened pigmented keel, bearing reversed cup-like apex. Middle part membranous, with internal sac pigmented in apical part, no basal thorns present. Phallobase ring-like, without extensive membrane. Ovipositor with long slender valvifers, sometimes connected at bases. Vagina long, *slender, lateral accessory glands inserted dorsally, bases of glandular ducts more sclerotized,* unpaired apical gland short. Spermaduct short, straight, spermatheca robust, with Y-shaped gland.

Distribution. The only known species originates from the Mysool Island. Additional not yet described species were found in the collection of New Guinean Lycidae from MNHH.

Metriorrhynchini incertae sedis

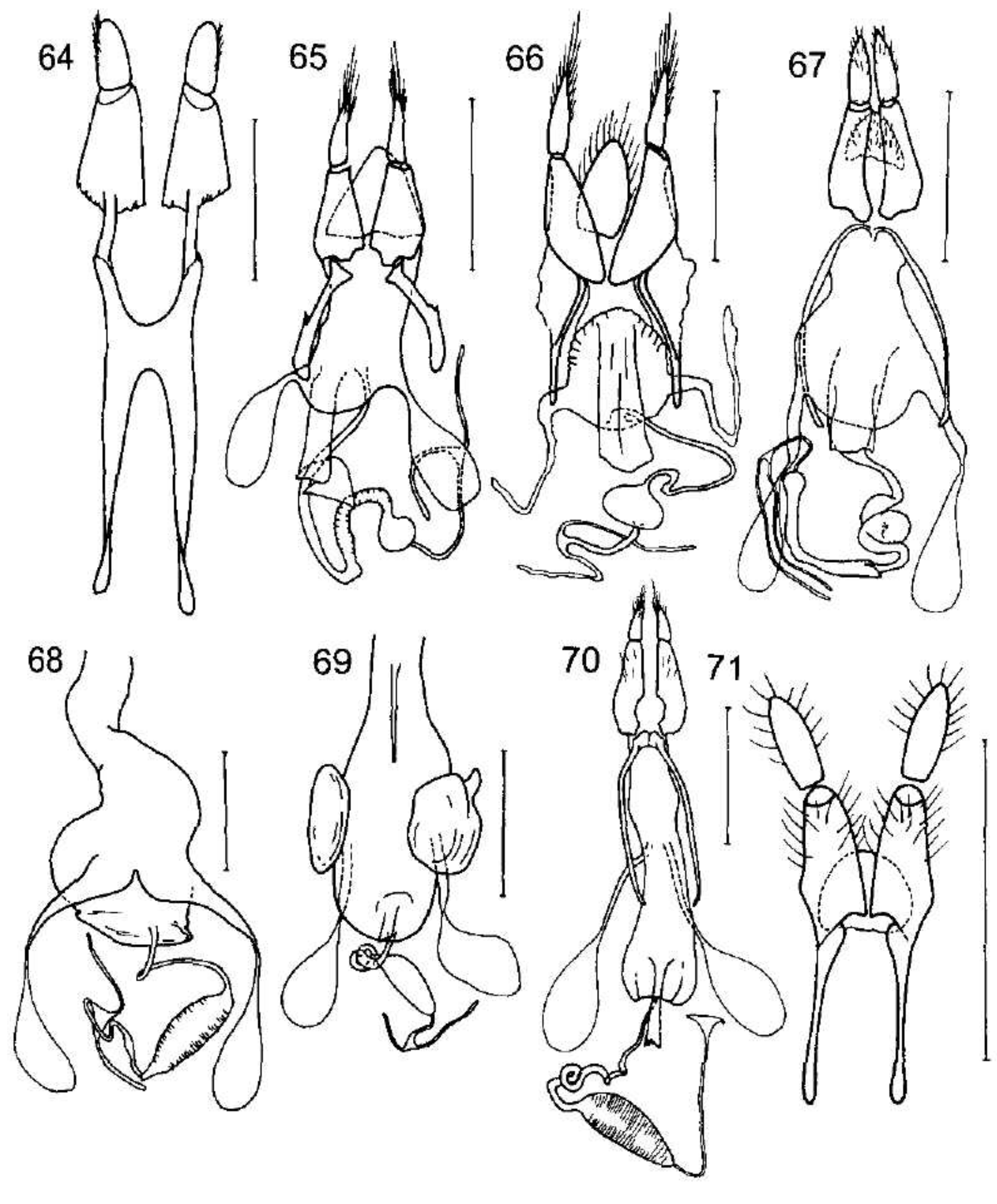
Leptotrichalus Kleine, 1925
(Figs 14, 28, 38, 55, 66)

Leptotrichalus Kleine, 1925: 296 (type species: *Metriorrhynchus cyaniventris* Kirsch, 1875, by original designation).

Diagnosis. Pronotum slender (Fig. 38), apparently longer than wide with one longitudinal median areola, first elytral primary costa shortened, internal sac of male genitalia without any thorns. Ovipositor with short valvifers, lateral glands of vagina attached laterally (Fig. 66).

Redescription. Body medium sized to large (5–22 mm), slightly dorsoventrally flattened, slender, moderately to considerably widened backwards. Dorsal side (pronotum and elytra) often yellow (species distributed on the Philippines and Sulawesi) or dark brown to black (species from Borneo, Sumatra and continental Malaysia).

Head small, partly covered by pronotum, hypognathous, with more or less developed rostrum, antennal tubercles moderately prominent, depression behind them shallow, gula longer than wide,



Figs 64–71 64 – Ovipositor of *Trichalus flavopictus* Waterhouse, 65–67 Ovipositor and genital ducts 65 – *Lobatang miserandus* (Kleine), 66 – *Leptotrichalus accomodatus* Kleine, 67 – *Diatrichalus ruficollis* Bocák, 68–69· Female genital ducts 68 – *Trichalus flavopictus* Waterhouse, 69 – *Microtrichalus retractus* Bocák, 70 – Ovipositor and genital ducts of *Emclases subelectus* Bocák et Bocáková, 71 – ovipositor of *Enylus* sp. Scales 0.5 mm

posterior tentorial pits apparent, tentorial arms sclerotized, widened to the apex, mouth parts small, but all parts well developed, clypeus narrow (as a consequence of presence of rostrum), concave, labrum narrowed frontally, without any emargination in apical part, lateral arms connecting epipharynx with labrum vestigial, much shorter, connected very closely with labrum. Mandibles shorter than labrum, tiny, slender at apex. Labium with robust praementum and tiny, U-shaped postmentum; praementum firmly connected with well sclerotized hypopharynx. Labial palpi slender, apical palpomere nearly parallel-sided, only slightly narrowed to apex, apical palpomere longest of all Maxillae with well developed, robust cardo (up to one third of stipes length); galea very long, much longer than combined length of cardo and stipes, with well sclerotized basal part, lacinia present but with much shorted setae, maxillary palpi slender, apical palpomere slender, longest, compressed, approximately parallel-sided. Antennae compressed, antennomeres 3–10 parallel-sided to slightly serrate, never flabellate, densely pubescent. Eyes large, hemispherically prominent. Pronotum slender, always longer than wide at base, narrowed frontally, only very slender longitudinal areola developed in middle of pronotum, sometimes less apparent lateral carinae present in middle of pronotal length. Basisternum slender, with strong longitudinal keel, basisternal processes long. Mesoscutellum slightly emarginate at apex. Mesosternum very wide in distal part, mesepimeron robust, strongly convex, projected. Metanotum wider than long, without emargination at apical margin, postnotum with apparent keel. Elytra slender, flat, with well developed secondary costae in all species. Abdomen usually slender, much more narrowed than elytra, not reaching their apex. Legs very long, slender, strongly compressed.

Male genitalia very diverse in shape, often slender, tube-like, internal sac without any basal thorns, rarely with strengthened sclerotized parts. Phallobase often with large well sclerotized membrane. Ovipositor with short valvifers, connected with coxites by membrane, vagina short, accessory glands attached laterally, unpaired vaginal gland large, spermaduct slender, spermatheca bulb-like.

DISTRIBUTION. Most species of this specious genus occur in the Philippines. Further representatives are known from Peninsular Malaysia, Sumatra, Borneo, Java, western part of the Lesser Sundas (Bali, Lombok, Sumbawa) and Celebes. They were not reported from the Moluccas or eastern part of the Lesser Sundas (from Komodo and Flores to Timor). *Leptotrichalus leveri* Kleine is reported from Solomon Islands but these species is not in fact congeneric with *Leptotrichalus* (see *Microtrichalus*).

***Lobatang* gen. n.**

(Figs 6, 22, 26, 32–33, 40–41, 52, 61–62, 65)

TYPE SPECIES *Lobatang papuensis* sp. n.

DIFFERENTIAL DIAGNOSIS. Externally very similar to *Trichalus* (general body form, shortened first elytral primary costa, only one longitudinal areola in middle of pronotum, Figs 40–41). Male genitalia are very different, internal sac is completely sclerotized (Fig. 52,61–62), very characteristic for whole genus. Lateral glands of vagina are inserted laterally (Fig. 65), valvifers of ovipositor are very stout, short. Mandibles slender, sickle-like (Fig. 6).

DESCRIPTION. Body medium-sized to moderately large (7.5–13.0 mm), dorsoventrally flattened, parallel-sided to slightly widened backwards. Most species dark brown, some with light coloured elytra.

Head small, hypognathous, without rostrum, antennal tubercles moderately prominent, followed by shallow transverse depression behind them, gula transverse, gular sutures unapparent, distance between them longer than length of gula. Eyes large, hemispherically prominent. Posterior tentorial arms well sclerotized. Clypeus concave, labrum with bent lateral margins, wider than long, slightly emarginate at apex, lateral arms long, similar as in *Diatrichalus*. Epipharynx deeply emarginate at apex, hypopharynx short, as long as labrum wide, quite slender, frontal margin concave, lateral processes slender. Mandibles slender, sickle-like. Praementum robust, postmentum V-shaped, well developed, labial palpomere 2 longest of all, apical palpomere widened. Maxillae with small cardo and robust plate-like stipes, galea well developed, as long as palpomere 2 of maxillary palpi, apical palpomere slender, only in one species inner margin of apical palpomere slightly convex, a bit stronger in basal third, obliquely cut at apex. Antennae long, strongly compressed, reaching two thirds to three quarters of elytral length, antennomeres 3–10 nearly parallel-sided to serrate in both sexes. Pronotum flat, with one longitudinal areola in middle, sometimes lateral margins nearly parallel or pronotum much wider at base, basisternum trapezoidal, much narrower at apex, apical processes robust, short, frontal margin of proepisternum slightly concave. Metascutellum slightly emarginate at apex, lateral processes long, quite slim. Mesosternum connected with metasternum through narrow keel. Frontal margin only slightly concave. Hind margin of metascutellum simple, straight, without apparent keel, postnotum bilobed with longitudinal keel. Elytra flat, with shortened primary costa 1, usually with well developed secondary costae, in one species secondary costae apparently weaker than transversal ones, irregular, missing in some places. Legs long, slender, hind trochanters much wider in apical part.

Male genitalia very specific and uniform within genus. Phallus robust only at base, slender and only very gradually narrowed in apical two thirds, internal sac completely sclerotized, in apical one tenth slightly widened, and provided with dense setae. Phallobase annuliform, robust, membrane partly sclerotized. Ovipositor short and wide, valvifers robust, laterally connected with coxites by membrane, vagina wide, accessory glands inserted laterally, glandular ducts very short, unpaired apical gland nearly as long as vagina.

NAME DERIVATION. "*Lobatang*" is a shortened form derived from the local name Gunung Lompobatang (Sulawesi) where Dr L. J. Toxopeus collected in 1936 the second recognized species of this genus (*Trichalus miserandus* Kleine, 1939). "*Lobatang*" is a noun of masculine gender.

DISTRIBUTION The genus Lobatang gen. n. is known from New Guinea and Sulawesi.

REMARK. Two species originally placed to the genus *Trichalus* should be classified with the genus *Lobatang* gen. n. They are *Lobatang sordescens* (Bourgeois, 1900) from New Guinea and *Lobatang miserandus* (Kleine, 1939) from Celebes. Their redescriptions are given further.

***Lobatang papuensis* sp. n.**

(Figs 6, 33, 61)

TYPE MATERIAL. holotype, male, "Irian Jaya Jayawijaya, Bime, 1600–1900 m 11. 9. 1993, leg A Riedel" (SMNS), paratypes, 1female, "Irian-Jaya, Prov Jayawijaya, Nalca, 8 9. 1992" (SMNS), 1 male, the same locality data as holotype, 22 9 1993 (LMBC), 1male, the same locality data as holotype (SMNS)

DIFFERENTIAL DIAGNOSIS. *Lobatang papuensis* sp. n. is the only species of the genus with light basal part of elytra. Moreover it has the smallest eyes compared with related species.

DESCRIPTION. Body moderately large, dark brown to black, only basal part of elytra light yellow. Head small, antennal tubercles extensive but flat, depression behind them shallow. Eyes hemispherically prominent, their distance 1.11 times bigger than eye diameter. Maxillary palpi slender, apical palpomere nearly parallel-sided, antennae serrate, long, strongly compressed, reaching three quarters of elytral length. Scutellum only very slightly emarginate at apex. Elytra approximately parallel-sided, all primary costae equal in strength, primary costa 3 shortest, transverse costae fine, dense. Secondary costae fully developed, at least as strong as transverse ones. Legs long, slender. Male genitalia as in Fig. 61.

Measures (male, holotype). Body length 11.8 mm, width at humeri 2.65 mm, eye diameter 0.66 mm, distance of eyes 0.73 mm.
Name derivation. The specific name refers to the distribution of this species.

Lobatang acuticornis sp. n.

(Figs 32, 41, 52)

Type material. holotype, male, "Irian Jaya: Prov. Jayawijaya, Wamena, Angguruk-Tanggeam, 1500–1800 m, 28. 9 1991, leg. A Riedel" (SMNS).

Differential diagnosis. *Lobatang acuticornis* sp. n. is the only New Guinean species from this genus with reddish brown pronotum, from completely gray-brown *Lobatang sordescens* (Bourgeois, 1900)it differs also in the size of male eyes.
Description. Male, holotype. Body medium sized, flat, prothorax reddish brown, rest of body dark brown to black, trochanter light brown. Head small, antennal tubercles conspicuous, eyes moderately large, 1.04 bigger than maximum distance between them. Maxillary palpi slender, antennae slender, compressed, only apical part of antennomeres 3–10 shortly projected. Pronotum with sharp, prominent anterior angles, hind angles very slender, acutely projected, pronotum considerably wider at base than long in middle. Elytra flat, primary costa 1 shortened, remaining equally strong, secondary costae developed in whole length, fine, transverse costae dense and regular. Male genitalia as in Fig. 52.
Measures (male, holotype). Body length 8.95 mm, width at humeri 1.92 mm, eye diameter 0.55 mm, distance of eyes 0.53 mm.
Name derivation. The name "*acuticornis*" refers to the acutely projected posterior angles of pronotum.

Lobatang sordescens (Bourgeois, 1900), comb. n.

(Figs 26, 62)

Trichalus sordescens Bourgeois, 1900 426.

Material examined Holotype, male, "Nuova Guinea, Fly River, L. M. d'Albertis, 1876–77" (MSNG)

Differential diagnosis. *Lobatang sordescens* is the only New Guinean species with completely gray-brown body and extraordinary large eyes of male.
Redescription. Male. Body rather robust, dark brown, elytra gray-brown, legs a bit lighter. Head small, with big prominent eyes, 1.26 times bigger than their maximum distance, antennae slender, only very slightly serrate, maxillary palpi slender. Pronotum flat, posterior angler strongly produced, anterior margin distinctly emarginate in middle, elytra slightly widened backwards, secondary costae fully developed. Male genitalia as in Fig. 62. Female unknown.
Measures (male, holotype). Body length 8.50 mm, width at humeri 2.15 mm, eye diameter 0.63 mm, distance of eyes 0.50 mm.

Lobatang miserandus (Kleine, 1939), comb. n.

(Figs 22, 40, 65)

Trichalus miserandus Kleine, 1939. 17.

Material examined Holotype, female, "Dr. L. J. Toxopeus, Zuid-Celebes, vi. 1936, G. Lompobatang, Malino, 1000 m" (ZMPA) Only one specimen designated as holotype has been found in Kleine's collection in Warsaw. Kleine (1939) cited "1male, female"

DIFFERENTIAL DIAGNOSIS. *Lobatang miserandus* is the only species of the genus known from Sulawesi, it differs from all related species in very weak secondary costae on elytra and in coloration.
REDESCRIPTION. Female. Body slender, medium sized, dark brown, only prothorax including pronotum, mesothorax, antennomere 2 and base of antennomere 3, trochanters and bases of femora lighter. Basal third of elytral suture with lighter pubescence. Head small, palpi slender, apical palpomere parallel-sided, antennae strongly compressed, antennomeres 3–5 parallel-sided, antennomeres 4–10 slightly serrate. Pronotum flat, anterior angles distinctly rounded, lateral margins parallel in frontal part, widened towards base. Elytra slightly widened, primary costa 1 shortened, costa 2 much weaker than costae 3 and 4, costa 3 longest reaching apex of elytra. Secondary costae developed but irregular, sometimes weaker than transversal ones, missing locally. Legs slender, strongly compressed. Male unknown.
MEASURES (holotype, female). Body length 10.2 mm, width at humeri 2.15 mm, eye diameter 0.42 mm, distance of eyes 0.59 mm.

Key to species of the genus *Lobatang* gen. n.

1 Elytral primary costa 2 much weaker than costae 3 and 4, primary costa 3 longest, reaching apex of elytra, secondary costae weak, locally missing. Sulawesi. .... *L. miserandus* (Kleine, 1939)
– Elytral primary costa 2 as strong as costae 3 and 4, primary costa 3 shortest, weaker in apical part of elytron. New Guinea 2
2. Basal part of elytra (one half to four fifths) light yellow. .... *L. papuensis* sp. n.
– Whole elytra concolor. 3
3 Whole upper side of body gray-black, eyes very large, 1.26 times bigger than maximum distance between them, base of phallus robust (Fig. 62) .... *L. sordescens* (Bourgeois, 1900)
– Pronotum reddish brown, head and elytra dark brown to black, eyes smaller, 1.04 times bigger than maximum distance between them. .... *L. acuticornis* sp. n.

Diatrichalus Kleine, 1926
(Figs 1–3, 7, 18–19, 30, 37, 42, 53, 67)

Diatrichalus Kleine, 1926: 167 (type species: *D. xylobanoides* Kleine, 1926, by original designation)
Mimotrichalus Pic, 1930: 92, hors texte – **syn. n.** (type species: *M. tenimberensis* Pic, 1930, by monotypy).

DIAGNOSIS. Pronotum with median lanceolate areola only, lateral carinae missing (Fig. 37), elytra with shortened primary costa 1, antennae of both sexes more or less acutely serrate, but never flabellate, phallus stout, apical part projected, internal sac prolonged, more or less sclerotized (Fig. 53), vaginal glands inserted laterally, spermatheca long, slim, rod-like (Fig. 67).
REDESCRIPTION. Body medium-sized, dorsoventrally flattened, coloration variable but considerable part of species black or black with metallic blue shine, part with brightly colored pronotum and basal part of elytra. Never light concolor.

Head small, hypognathous, partly concealed by pronotum, cranium compact, without rostrum, gular sutures unapparent, distance of posterior tentorial pits bigger than the length of gula, posterior tentorial arms slim, eyes prominent, usually smaller than their frontal distance. Mouth parts well developed, mandibles stout, curved in right angle, more than twice longer than labrum, labrum wider than long, emarginate in distal part, lateral processes long, epipharynx large, with sparse setae, hypopharynx flat, lateral processes weak, apical part less sclerotized; labium with robust praementum, postmentum very tiny, labial palpi with apical palpomere robust, widest at apex, with irregular unpigmented papillae at apical margin. Maxillae with small cardo (one fifth of stipes length), lacinia very reduced, only membrane and several setae present, lacinia well developed, membranous, with less numerous setae, maxillary palpi with broad apical palpomere bearing papillae at apex Antennae strongly compressed, serrate in both sexes or shortly flabellate in male in some species Pronotum usually wider than long, with one more or less broad longitudinal areola in the middle, lateral margins often elevated, basisternum trapezoidal, relatively broad Mesosternum narrowly connected with metasternum, metascutellum slightly emarginate at apex Postnotum without keel Elytra flat, secondary costae irregular to completely absent in some species, costa 2 and 3 often fused before apex Legs often relatively strong and short, strongly compressed

Male genitalia always with relatively short and robust phallus, apical part ventrally projected, hiding apical opening, internal sac without pair basal thorns, nearly always strongly sclerotized in apical part, phallobasal membrane sometimes extensive but never sclerotized Ovipositor with slender, long valvifers, sometimes incompletely fused at base, vagina relatively short, basal part of glandular duct sometimes robust, accessory glands inserted laterally Spermaduct robust at base, spermatheca slender, very long

Distribution *Diatrichalus* is very widely distributed and its range coincides with the range of Trichalinina

Remark Kleine (1926) restricted *Diatrichalus* for species with missing secondary elytral costae only but the secondary costae are very often only partly missing or transversal costae are Y-shaped and consequently interrupted secondary costa results from this pattern The only sure distinguishing characters are those in male and female genitalia as given in the differential diagnosis, and therefore many species described as *Trichalus* because of their fully developed secondary costae belong in fact to the genus *Diatrichalus* Pic never studied genitalia and his classification is confused All types described by both Pic and Kleine should be studied for proper generic classification in the future The genus *Diatrichalus* in the sense as presented here includes many species occurring mostly in the Papuan subregion and it is probable that the total number of species in this genus will exceed one hundred in very short time as a result of transfers from *Trichalus* and descriptions of new species from available collections (Bocak, unpubl)

Enylus C. O. Waterhouse, 1879

(Figs 11, 29, 35, 54, 71)

Enylus Waterhouse, 1879 7 (type species *E segregatus* Waterhouse, 1879, by monotypy)

Diagnosis Pronotum with median lanceolate areola only (Fig 35), lateral carinae missing, elytra with fully developed four primary costae, antennae of both sexes slightly serrate or antennomeres nearly parallel-sided, never flabellate, phallus slender (Fig 54), vaginal glands inserted laterally, spermatheca long, slim, rod-like

Redescription Body small to medium sized, dorsoventrally flattened, known species are concolor dark brown

Head small, hypognathous, partly concealed by pronotum, cranium compact, without rostrum, gular sutures apparent, distance of posterior tentorial pits bigger than the length of gula, posterior tentorial arms slim, eyes prominent, usually smaller than their frontal distance Mouth parts well developed, mandibles stout, curved in right angle, relatively short, slightly longer than labrum, labrum wider than long, emarginate in distal part, epipharynx membranous, hypopharynx plate-like, labium with robust praementum, postmentum small, with short anterior processes, labial palpi with apical palpomere robust, widest in apical half Maxillae with small cardo, lacinia reduced, only membrane and several setae present, lacinia well developed, membranous, relatively short but wide, maxillary palpi robust, apical palpomere obliquely cut at apex, broad Antennae strongly compressed, serrate in both sexes Pronotum usually wider than long, with longitudinal areola in the middle Basisternum trapezoidal, relatively broad Mesosternum narrowly connected with metasternum, metascutellum straight, without keel Postnotum with keel Elytra flat, secondary costae well developed, regular, primary costa 1 developed in whole length, costae 2 and 4 much stouter than costae 1 and 3, costa 3 much weaker in apical part Legs slender, strongly compressed

Male genitalia always with slender, long phallus, with pair of basal thorns, partly sclerotized in apical part, phallobasal membrane inconspicuous Ovipositor with short, rather stout valvifers, vagina relatively short, bases of glandular ducts robust, accessory glands inserted laterally Spermaduct slender, simple, spermatheca slender, very long

Distribution The genus *Enylus* is known from New Guinea and Australia

Remark The genus *Enylus* has been classified by Kleine (1933) within the tribe Trichalinina and transferred by Bocák & Bocaková (1990) to the subtribe Metriorrhynchinina *Enylus* was included in the performed phylogenetic analysis and it has been proved that this genus is not closely related to the monophylum *Flabellotrichalus* + *Microtrichalus* + *Trichalus* + *Schizotrichalus* + *Enicl*a*ses* *Enylus* is connected with *Diatrichalus* by the presence of long spermatheca and the shape of mandibles, but only the shape of mandibles is an exclusively shared synapomorphy In spite of long searching no other persuading unique synapomorphy has been found Actually the genus *Enylus* was kept together with the group of genera with shortened first elytral primary costa and laterally attached glands of vagina and his position within Metriorrhynchini can be elucidated within a complex revision of the whole tribe only During this study several not yet described species were found in some of studied collections (MNHH and SMNS) which exhibit a high degree of diversification (Bocak, unpubl)

Therefore it is supposed that in the future classification of this group several new genera will be proposed

***Kassemia* gen. n.**

(Figs 4, 23–24, 48, 51, 60, 63)

Type species *Kassemia oculata* sp n

Diagnosis The combination of seven areolae of the pronotum, complete absence of elytral secondary costae (Fig 48) and shortened first elytral primary costa enable sure identification of this genus The shape of male antennae shows low degree of relationship with other genera with shortened primary costa 1 (Figs 23–24)

Description Body small to medium sized, parallel-sided, all representatives dark brown to brown with humeral quarter to half of elytra light yellow to brown, always apparently much lighter than the rest of elytra

Head small, hypognathous, partly concealed by pronotum, cranium without rostrum, gular sutures unapparent, distance of posterior tentorial pits bigger than the length of gula, posterior tentorial arms slim, eyes prominent, their size variable within genus Mouth parts well developed, mandibles slender, long, three times longer than labrum, labrum wide, apparently emarginate in distal part, with long setae at apex, labium with robust praementum, postmentum very well developed, plate-like, labial palpi with apical palpomere robust, securiform Maxillae with small cardo, lacinia very reduced, only membrane and several setae present, lacinia well developed, very wide but short, membranous, with dense setae, maxillary palpi with broad apical palpomere Antennae strongly compressed, flabellate in males and serrate in females Pronotum usually wider than long, with seven areolae arranged as in Fig 34, basisternum trapezoidal, much narrower at apex than in base Mesosternum widely connected with metasternum, metascutellum slightly emarginate at apex Postnotum without keel Elytra flat, secondary costae completely absent, costa 2 and 3 sometimes fused before apex Legs often relatively strong and short, strongly compressed

Male genitalia with relatively short and robust phallus, apical part widely open, internal sac strengthened at base in thorns-like structure, internal sac with tiny pigmented papillae at apex, phallobasal membrane never sclerotized. Ovipositor with slender, long valvifers, vagina as long as valvifers, widest at apex, accessory glands inserted laterally.
DISTRIBUTION. The genus *Kassemia* gen. n. is known from northeastern New Guinea only.
NAME DERIVATION. The name "*Kassemia*" is derived from the local name "Kassem Pass", where one specimen was collected. "*Kassemia*" is considered to be noun of feminine gender.

Kassemia oculata sp. n.

(Figs 4, 23, 63)

TYPE MATERIAL. holotype, male, "New Guinea, NE, Wau, 1200–1300 m, 22. x. 1965, J. Sedlacek Collector Bishop Mus." (BPBM). Paratype, 1 male, "NE New Guinea, Wau, Big Wau Ck., 1200 m, ix. 1965, P. Shanahan, Collector Bishop" (LMBC)

DIFFERENTIAL DIAGNOSIS. *Kassemia oculata* sp. n. differs from sympatrically occurring similar *K. wauensis* sp. n. in having the much bigger male eyes. The frontal part of pigmented area of internal sac is without deep emargination (Fig. 63).
DESCRIPTION. Male. Body medium sized, nearly parallel, dark brown, only basal palpalpomeres, trochanters and basal half of elytra light yellow, highest extent of dark part of elytra at suture. Head small, with extraordinary large hemispherically prominent eyes, maximum distance between eyes 1.51 times smaller than eye diameter, antennae flabellate, slightly reaching over half of elytral length, lamellae of middle antennomeres twice longer than antennomeral trunk. Pronotum with seven areolae, lateral carinae much weaker, less apparent, frontal margin convex, lateral ones nearly straight and parallel. Scutellum slightly emarginate at apex, elytra with four costae at base, costa 1 shortened, reaching one third of elytral length, costae 2 and 3 connected before apex, traversal costae strong, areolae apparently transverse. Phallus stout, with pigmented internal sac (Fig. 63). Female unknown.
MEASURES (male, holotype). Body length 6.75 mm, width at humeri 1.82 mm, width of pronotum 1.22 mm, length of pronotum 0.97 mm, eye diameter 0.62 mm, distance of eyes 0.41 mm.
NAME DERIVATION. The specific name refers to the extraordinary large eyes of male.

Kassemia rufithorax sp. n.

TYPE MATERIAL. holotype, female, "New Guinea, NE, Okapa, Purosa, 1700–2000 m, 18. i. 1966, J. Sedlacek, Collector Bishop Mus." (BPBM). Paratypes, 1 female, "New Guinea (NE), Wau, Morobe Distr. 1250 m, 5. ii. 1963, J. Sedlacek, Collector Bishop"; 1 female, "New Guinea, NE, Kassem Pass, 1350 m, 18. vii. 1963, J. Sedlacek, Bishop" (BPBM, LMBC).

DIFFERENTIAL DIAGNOSIS. *Kassemia rufithorax* sp. n. is the only species with light colored metathorax.
DESCRIPTION. Male unknown. Female. Body medium sized, parallel, mouthparts, trochanters, metathorax and basal half of elytra yellow, shape of border line between light and dark part of elytra variable. Head small, eyes hemispherical but their distance 1.88 times bigger than their diameter, antennae serrate, pronotum wider than long, with seven areolae, mat, densely pubescent, slightly narrowed to frontal part. Scutellum widely emarginate at apex. Elytra with four primary costae at humeri, secondary costae completely missing. Primary costa 1 reaching four fifth of elytral length, costa 3 a bit weaker in apical part, sometimes connected with costa 2.
MEASURES (female, holotype). Body length 8.50 mm, width at humeri 1.92 mm, width of pronotum 1.61 mm, length of pronotum 1.13 mm, eye diameter 0.34 mm, distance of eyes 0.64 mm.

NAME DERIVATION. The specific name refers to the color of metathorax.

Kassemia wauensis sp. n.
(Fig. 60)

TYPE MATERIAL: holotype, male, "New Guinea (NE), Wau, Morobe Distr. 1200 m, 4–5. ii. 63, J. Sedlacek , Collector Bishop" (BPBM); Paratypes, 2 males, "New Guinea, NE, Chimbu valley, 1800 m, 16 v. 1963, J. Sedlacek" (BPBM, LMBC)

DIFFERENTIAL DIAGNOSIS. The male of *Kassemia wauensis* sp. n. has much smaller eyes, the border between light and dark part of elytra in not so sharp as in the preceding species and the frontal part of pigmented area of internal sac has deep emargination (Fig. 60).

DESCRIPTION. Male. Body small, slender, dark brown to black, only humeral quarter of elytra light brown to yellow, trochanters a bit lighter than rest of legs. Head small, eyes prominent but small, distance between them 1.95 bigger than their diameter, antennae reaching very slightly over half of elytral length, flabellate, lamella of antennomere 3 slightly longer than antennomeral body, lamellae of middle antennomeres 1.5–1.7 times longer than antennomeral trunk. Pronotum with seven areolae, densely pubescent, mat, lateral margins nearly parallel. Apical emargination of scutellum shal-

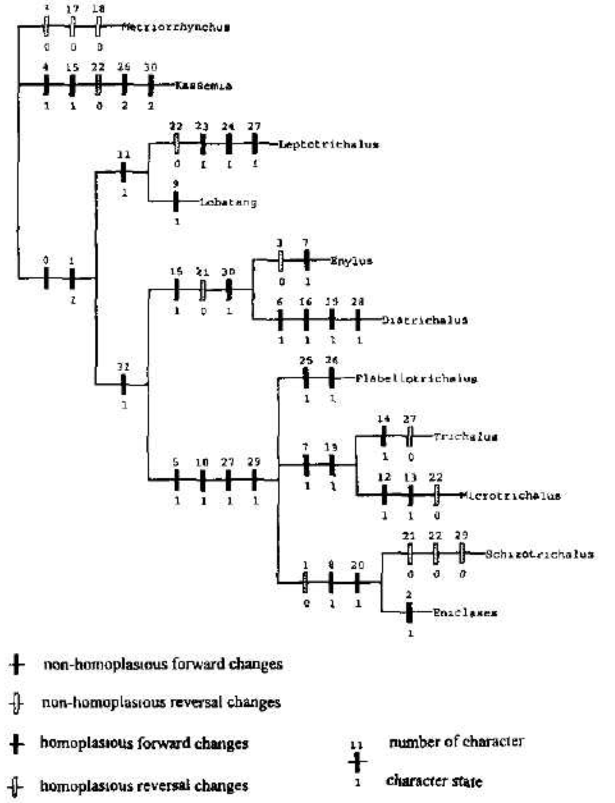


Fig 72 The strict consensus tree counted by the procedure Nelsen of Hennig86

low. Elytra with shortened primary costa 1, reaching one third to two fifth of elytral length, secondary costae missing, transverse costae regular, strong, areolae slightly transverse to square. Phallus stout, gradually narrowed to the apex. Female unknown.
MEASURES (male, holotype). Body length 4.32 mm, width at humeri 0.99 mm, width of pronotum 0.83 mm, length of pronotum 0.63 mm, eye diameter 0.20 mm, distance of eyes 0.39 mm.
NAME DERIVATION. The specific name reefers to the type locality of the holotype.

Kassemia sedlacekiae **sp. n.**
(Figs 24, 48, 51)

TYPE MATERIAL. holotype, male, "New Guinea, NE, Karimui, 1080 m, 14. vii 1963, M. Sedlacek, Bishop" (BPBM)

DIFFERENTIAL DIAGNOSIS. *Kassemia sedlacekiae* sp. n. is the only known species with brown humeral portion of elytra. Compared with remaining species of the genus it has a bit shorter first elytral primary costa; only seven to eight transversal costae are connected with first elytral primary costa in *K. sedlacekiae* sp. n. compared with 12 to 18 in other species (Fig. 48). Male genitalia as in Fig. 51.
DESCRIPTION. Male. Body slender, small, parallel, thorax and humeral part of elytra brown, head, middle part of pronotum, legs, antennae, scutellum and apical two thirds of elytra much darker brown. Head small, eyes prominent but rather small, their distance 1.29 times bigger than their maximum diameter, antennae flabellate, lamella of antennomere 3 1.4 times longer than body of antennomere, middle antennomere lamellae twice longer than antennomeral trunk. Pronotum with seven areolae, all pronotal carinae well developed, pronotum wider than long, posterior angles slightly projected. Elytra with four primary costae at humeri, primary costa 1 very short, only one fifth of elytral length long, secondary costae missing, transversal costae, stout, regular, areolae transverse to square. Phallus short, stout, nearly parallel-sided. Female unknown.
MEASURES (male, holotype). Body length 6.00 mm, width at humeri 1.49 mm, width of pronotum 1.26 mm, length of pronotum 0.92 mm, eye diameter 0.38 mm, distance of eyes 0.49 mm.
NAME DERIVATION. The specific name is a matronym in honor of Mrs. Marie Sedláčková (Australia) who collected the unique specimen of this new species.

Key to species of the genus *Kassemia* gen. n.

1 Metathorax yellow . . . . *Kassemia rufithorax* sp. n.
– Metathorax dark brown to black. 2
2 Eyes extra large, 1.51 times larger than the maximum distance between them . . *Kassemia oculata* sp. n.
– Eyes much smaller, their distance 1.29–1.95 times bigger than their maximum diameter. 3
3 Eyes smaller, their distance 1.95 times bigger than their maximum diameter, humeral quarter of elytra light yellow, rest of elytra dark brown to black, more than eleven transversal costae connected with first elytral primary costa . . . . *Kassemia wauensis* sp. n.
– Eyes rather larger, their distance 1.29 times bigger than their maximum diameter, humeral third of elytra brown, slightly lighter than the rest of elytra, only 7–8 transversal costae connected with first elytra primary costa . . . . *Kassemia sedlacekiae* sp. n.

Key to genera of Metriorrhynchini with shortened first elytral primary coxa

1 Pronotum with seven areolae (the same type of arrangement as in *Metriorrhynchus*, Fig. 34), only three longitudinal elytral costae (costa 2, 3 and 4) present in the middle of each elytron; costa 1 shortened (Fig. 48), antennae flabellate (Figs 23–24) . . . . **Kassemia** gen. n.
– Pronotum with less than seven carinae 2

2. Pair of vaginal glands inserted dorsally (Figs 68–70), apical part of phallus narrower than middle part, ventrally open, only dorsal part sclerotized (Figs 56–59) 3

– Pair of vaginal glands inserted laterally, apical part of phallus as wide as middle part 7

3. Pronotum with one lanceolate longitudinal areola attached to frontal and basal margin of pronotum in one point (Fig 35) 5

– Pronotum with five areolae or with two anteriorly divergent longitudinal carinae (Fig. 39). 4

4 Pronotum with five areolae (Fig 36). .... ***Schizotrichalus*** Kleine, 1926

– Pronotum with two anteriorly divergent longitudinal carinae (Fig 39). .... ***Eniclases*** Waterhouse, 1879

5 Male antennae flabellate .... ***Flabellotrichalus*** Pic, 1921

– Male antennae serrate or antennomeres parallel-sided. 6

6 Vagina with two lateral pocket in middle part and with unpaired very slim and long gland in basal part (Fig. 69), valvifers slender, usually free, sometimes connected in basal part .... ***Microtrichalus*** Pic, 1921

– Vagina without lateral pockets, unpaired gland missing, valvifers robust, connected subbasally (Fig 64) .... ***Trichalus*** Waterhouse, 1877

7 Maxillary and labial palpomeres with apparent sensilae, apical palpomeres broad, securiform (Fig. 19), apical part of phallus projected ventrally, internal sac very complex, sclerotized (Fig 53) .... ***Diatrichalus*** Kleine, 1926

– Maxillary and labial palpomeres slender, internal sac often without sclerotization, but sometimes completely sclerotized 8

8 Pronotum very slender, longitudinal areola very slender (Fig. 38) .... ***Leptotrichalus*** Kleine, 1925

– *Pronotum approximately as wide as long, internal sac completely sclerotized, very slender, basally attached to* phallus (Figs 52, 61–62). .... ***Lobatang*** gen n.

Ditoneces **Waterhouse, 1879**

(Erotinae: Platerodini)

Ditoneces Waterhouse, 1879 31 (type species· *Lycus punctiventris* (Waterhouse, 1878), by subsequent designation)
Falsotrichalus Pic, 1921, **syn. n.**
Falsotrichalus Pic, *1921* 3, hors texte (type species: *F. gracilicornis* Pic, 1921, by monotypy), **syn. n.**
Ditoneces gracilicornis (Pic, 1921) **comb. n.**

I have found that the genus *Falsotrichalus* belongs to the subfamily Erotinae and it is a junior subjective synonym of the genus *Ditoneces*.

Acknowledgements

I extend my grateful thanks to the following entomologists who have been very kind to lend me type specimens or *other material from their institutions or private collections listed under depositories.* J Beard (London), K Matsuda (Takarazuka City), M. Brancucci (Basel), J. J Ménier (Paris), G A. Samuelson (Honolulu), S Kasantsev (Moscow), R Poggi (Genova), W Schawaller (Stuttgart) and S. A. Ślipiński (Warsaw) I am also very obliged S A Ślipiński for his help and advice Preparation of the final form of this manuscript was supported by the grant of Czech Grant Agency, number 206/98/0539.

REFERENCES

BOCAK L & BOCAKOVA M 1990 Revision of the supergeneric classification of the family Lycidae (Coleoptera). *Pol Pismo Entomol* **59**: *623–676*

BOCAK L & BOCAKOVA M. 1991· Revision of the genus Eniclases Waterhouse, 1879 (Coleoptera, Lycidae, Metriorrhynchinae) *Mitt Münch Entomol Ges.* **81** 203–226

BRANCUCCI M. 1980 Morphologie comparée, évolution et systématique des Cantharidae (Insecta· Coleoptera) *Entomol Basil* 5. 215–388.

BLANCHARD E *1856 Voyage de M'Dumont d'Urville ... Vol. iv, Zoologie Insectes.* Paris· Didot, 422 pp

BOISDUVAL J B A 1835: *Faune entomologique de l'Oceanie, comprenant les Coleopteres, les Hemipteres, les Nevropteres, les Hymenopteres et les Dipteres Bd 1.* Paris Roret, 267 pp

BOURGEOIS J 1891 Études sur la distribution géographique des Malacodermes I. Lycides *Ann Soc Entomol. Fr* **60**. 337–364

BOURGEOIS J 1900 Lycides nouveaux ou peu connus de Musee de Genes Deuxieme memoire *Ann Mus Civ Stor Natur Genova* **21** 420-432

ERICHSON W F 1842 Beitrag zur Fauna von Vandiemensland, mit besonderer Ruecksicht auf die geographische Verbreitung der Insecten *Weigeman Arch* **8** 83–287

FABRICIUS J C 1775 *Systema Entomologiae, sistens insectorum classes ordines genera species adiectis synonymis locis, descriptionibus, observationibus* Flensburgi et Lipsiae Korte, xxvii + 832 pp

FAIRMAIRE L M 1877 Diagnoses des Coleopteres australiens et melanesiens *Petit nouv entomol* **2** 166–167

FAIRMAIRE L M 1879 Descriptions de Coleopteres nouveaux ou peu connus du Musee Godeffroy *Journ Mus Godeffroy* **14** 80–114

FARRIS J S 1988 *Hennig Hennig86 reference Version 1 5 manual* Computer program and manual distributed by the author

CROOK K A W 1981 The break-up of the Australian-Antarctic segment of Gondwanaland Pp 1–20 In KEAST A (ed) *Ecological Biogeography of Australia Vol 3* The Hague-Boston-London Dr W Junk Publishers 785 pp

KIRSCH T 1875 Neue Kaefer aus Malacca *Mitt Zool Mus Dresden* **1** 25–58

KLEINE R 1925 Die neue Gattung Leptotrichalus *Philippine J Sci* **28** 295–311

KLEINE R 1926 Coleoptera, Lycidae *Nova Guinea* Résultats de l'expedition scientifique néerlandaise a la Nouvelle-Guinee **15**(2) 91–195

KLEINE R 1928 Neue Indische Lycidae nebst faunistische Bemerkungen *Indian Forest Rec* **13** 221–268

KLEINE R 1930 Bestimmungtabelle der Trichalusverwandschaft *Treubia* **11** 325–341

KLEINE R 1933 Lycidae Pars 128 Pp 1–145 In JUNK W & SCHENKLING S (eds) *Coleopterorum Catalogus* Berlin W Junk

KLEINE R 1936 Check list of Pacific Lycidae *Bernice Pauhu Bishop Mus Occ Pap* **12** 1–7

KLEINE R 1939 Neue Lyciden von den orientalischen Inseln und Molukken *Treubia* **17** 1–19

LEA A M 1909 Revision of the Australian and Tasmanian Malacodermidae *Trans Entomol Soc Lond* **1909** 45–106

MACLEAY W 1886 The insects of Fly River, New Guinea, "Coleoptera" *Proc Linn Soc N S Wales* (Ser 2) **1** 136–157

MACLEAY W 1887 The Insects of the Cairns District, Northern Queensland *Proc Linn Soc N S Wales* (Ser 2) **2** 211–238

PIC M 1921a Contribution a l'etude des Lycides *L Echange* **404** 1–4 (hors texte)

PIC M 1921b Contribution a l'etude des Lycides *L Echange* **406** 9 (hors texte)

PIC M 1923 Contribution a l'etude des Lycides *L Echange* **412** 36 (hors texte)

PIC M 1926 Contribution a l'etude des Lycides *L Echange* **425** 29–30 (hors texte)

PIC M 1930 Malacodermes exotiques *L Echange* **442** 92 (hors texte)

POWELL C M, JOHNSON B D & VEEVERS J J 1981 The Early Cretaceous break-up of Eastern Gondwanaland, the separation of Australia and India, and their interaction with Southeast Asia Pp 3–14 In KEAST A (ed) *Ecological Biogeography of Australia Vol 3* The Hague-Boston London Dr W Junk Publishers 785 pp

RAMOS T C 1997 *Tree Gardener 2 2* The program and manual distributed by the author Sao Paolo

STEENIS C G G J v 1979 Plant-geography of east Malesia *Bot J Linn Soc* **79** 97–178

WATERHOUSE C O 1877 A Monograph of the Australian species of the Coleopterous family Lycidae *Trans Entomol Soc Lond* **1877** 73–86

WATERHOUSE C O 1878 On the different forms occurring in the Coleopterous family Lycidae, with descriptions of new genera and species *Trans Entomol Soc Lond* **1878** 95–118

WATERHOUSE C O 1879 *Illustration of the typical specimens of Coleoptera in the collection of the British Museum Part I – Lycidae* London British Museum 93 pp

Acta Soc. Zool. Bohem. **62**: 201–206, 1998
ISSN 0862–5247

Three new species and new record of *Leistus* from North India and Tibet (Coleoptera: Carabidae: Nebriini)

Jan FARKAČ

Faculty of Forestry, Czech Agricultural University, Kamýcká 957, CZ–16521 Praha 6, Czech Republic
E-mail: farkac@lf.czu.cz

Received June 18, 1998; accepted September 24, 1998
Published October 30, 1998

Abstract. *Three new species of the genus Leistus* Froehlig, 1799, *belonging to the subgenus Evanoleistus* Jedlička, 1967, are described and illustrated: *Leistus harpagon* sp. n. (India: Himachal Pradesh), *L. natruc* sp. n. (India: Uttar Pradesh) and *L. nyingtri* sp. n. from China (Tibet). *L.* (*E.*) *championi* Andrewes, 1920 is recorded from the Meghalaya province (India) for the first time.

Taxonomy, new species, Coleoptera, Carabidae, *Leistus*, North India, Palaearctic region

INDEXES

antennal index: length of entennomere 5/ length of antennomere 3 = IA
pronotal index: width/length of pronotum = IPw/l
pronotal index two: maximum width of pronotum/basal width of pronotum = IPm/b
elytral-pronotal index: combined width of elytra/ width of pronotum = IE/P
elytral index: length/width of elytra = IEl/w

SYSTEMATICS

Leistus (*Evanoleistus*) *harpagon* sp. n.
(Figs 1, 4, 5, 10)

DESCRIPTION (habitus of holotype as in Fig. 10). Body length 8.6 mm (holotype) and 9.0 mm (paratype). Color piceous-black, tarsi, tibiae, antennae and maxillary appendages paler. Mandibles brownish. Eyes small. Head coarsely, sparsely and irregularly punctate dorsaly, frons irregularly furrowed. Mandibles long, with sharp apex. Gular setae situated on transverse carina. IA = 1.70–1.90.

Pronotum (Fig. 1) cordiform (IPm/b = 1.72–1.73). Marginal bead narrow, lateral margin at anterior angles slightly elevated, sinuated in front of posterior angles. Posterior angles elongate-rectangular. Disc convex, sparsely, irregularly, finely pnctate. Basal impressions distinct at posterior angles, coarsely punctate. IPw/l = 1.30–1.35.

Elytra. Oval, without humeri. Strial punctation coarse, very distinct, becomming finer toward apex of elytra. Lateral bead narrow, punctate. Elytra highest in posterior half (lateral view). IE/P = 1.37–1.40, IEl/w = 1.68–1.70.

Aedeagus (Figs 4, 5). Apex quite rounded, slightly rotated and curved toward left side.

AFFINITIES. *Leistus (Evanoleistus) harpagon* sp. n. is in its habitus similar to *L.* (*E.*) *loebli* Perrault, 1985, but the latter is smaller and lacks the punctation on the head and the disc of pronotum.

TYPE MATERIAL. Holotype. Male, labelled: N India, Himachal Pradesh, Rohtang Paß: Mahri, 3300–3600m, 22.vii.1989, leg. A. Riedel. In the collection of W. Heinz, Schwanfeld (Germany). Paratype. Female, labelled: Indien (Himachal Pradesh), Pir Panjal Range: Rohtang Paß, 3600–4000m, 25.vii.1980, leg. [W.] Heinz. In the collection of J. Farkač, Praha.

ETYMOLOGY. The specific epithet is that of Harpagon, the famous miser of Molière, in apposition; it refers to the difficulties connected with collecting the specimens.

***Leistus (Evanoleistus) natruc* sp. n.**

(Figs 2, 6, 7, 11)

DESCRIPTION (habitus of holotype as in Fig. 11). Body length 8.8–9.7 mm (holotype 9.2 mm). Color piceous-black, tarsi, tibiae, antennae, mandibles and maxillary appendages paler. Eyes normal. Vertex of head with two impressions situated closer to eyes. Mandibles narrow and long, with sharp apex. Gular setae situated on distinctive transverse carina. IA = 1.39–1.62.

Pronotum (Fig. 2) rounded, very narrow (IPw/l = 1.25–1.40, IPm/b = 1.82–2.02).

Lateral bead wide, equally wide throughout. Lateral margin evenly arcuate, slightly elevated in posterior half, only feebly sinuate in front of posterior angles. Posterior angles obtusely angulate. Basal impression punctate, distinct only at posterior angles.

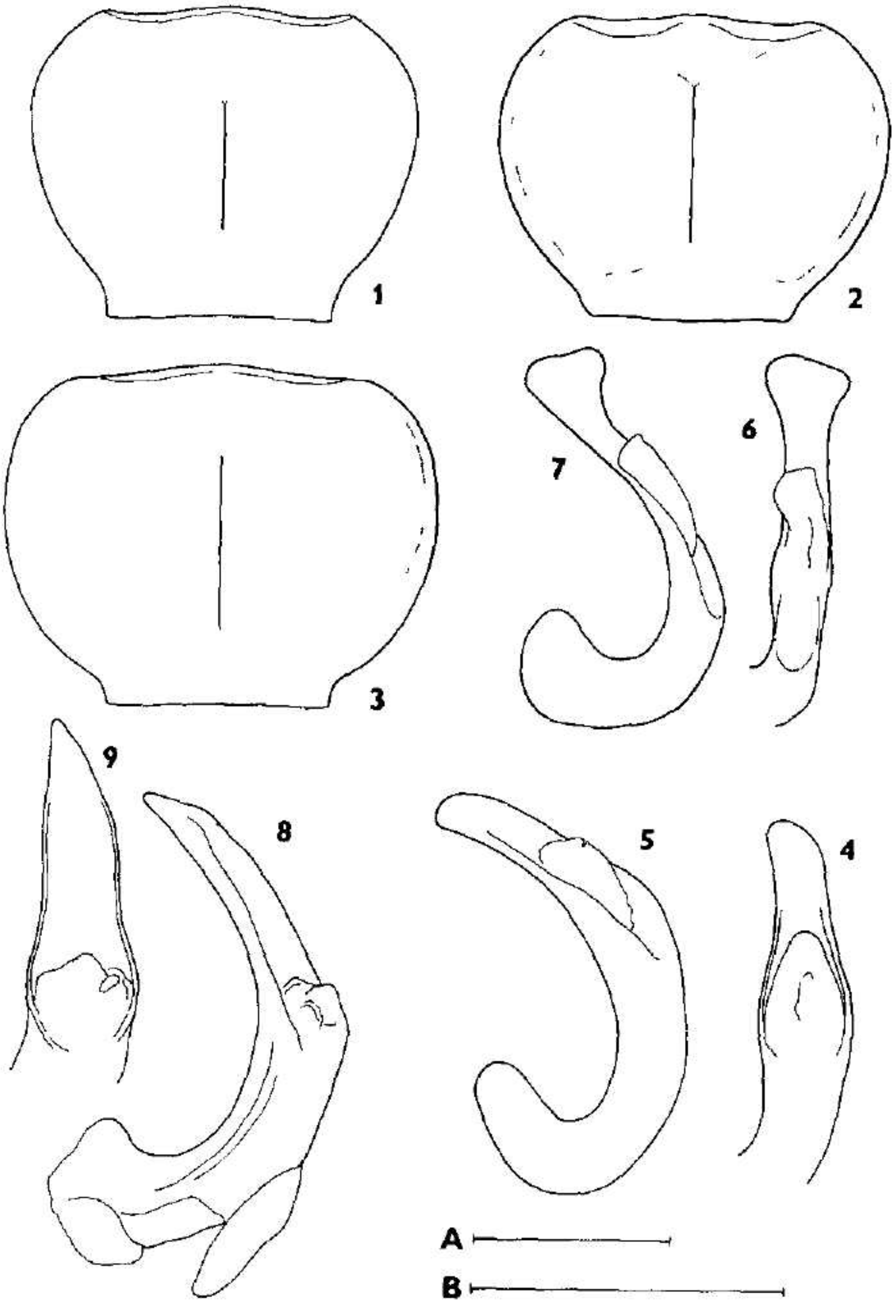
Elytra. Broadly oval, with evenly rounded humeri. Intervals flat, moderately distinct, finer at elytral apex. lateral bead narrow, lateral margin elevated in anterior half of elytra, particularly at shoulders. IE/P = 1.54–1.70, IEl/w = 1.48–1.58.

Aedeagus (Figs 6, 7). Asymmetrical in distal part, triangularly dilated toward right side and vaguely rotated upward toward right side.

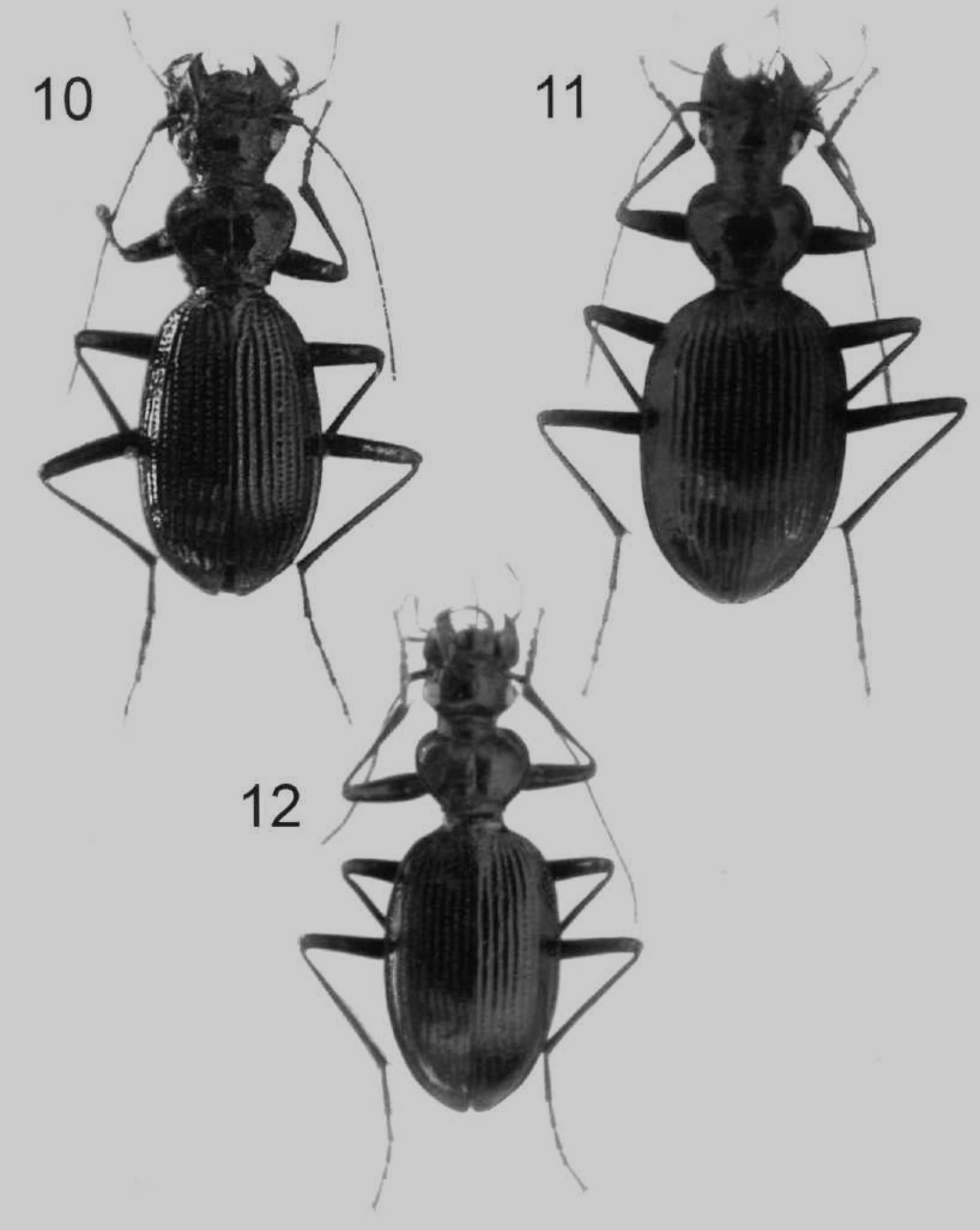
AFFINITIES. The southern part of the Palaearctic region, from Kachemire to Yunnan harbers several tens of mostly montane species of the genus *Leistus* Froehlig, 1799. Some of them are distinctive by the assymetrical, securiform distal portion of the aedeagus. The new species belongs to this group. Based on the asymmetrical portion of the aedeagus, *Leistus* (*Evanoleistus*) *natruc* sp. n. belongs in the relationship of *L.* (*E.*) *baudinoti* Deuve, 1985, *L.* (*E.*) *himalchuliensis* Perrault, 1986, *L.* (*E.*) *nepalensis* Jedlička, 1967, *L.* (*E.*) *pereaui* Perrault, 1986 (all from Nepal), *L.* (*E.*) *chalcites* Andrewes, 1936 from Sikkim, *L.* (*E.*) *taiwanensis* Perrault, 1986 from Taiwan, *L.* (*E.*) *yunnanus* Bänninger, 1925 from Yunnan and *L.* (*E.*) *brancuccii* Farkač, 1995 from Yunnan and Guizhou. Howewer, it differs from all these species by the markedly different shape of the pronotum (Fig. 2 and Deuve 1985, Farkač 1995: fig. 3, Perrault 1985a: fig. 4, Perrault 1985b: fig. 8 and 1986: figs 1–3 and 8). It differs from *Leistus championi* Andrewes, 1920, also that-occurs in Uttarpradesh, by the different shape of pronotum (Fig. 2 and Perrault, 1985b: fig. 3), and by the distinctly shorter, laterally less sinuate mandibles. It differs from *L.* (*E.*) *indus* Tschitschérine, 1903 by the slenderer form of the pronotum and aedeagus (Figs. 2, 6, 7 and Perrault 1985a: figs 7, 10–11). It is in its habitus similar to *L.* (*E.*) *nyingtri* sp. n., but it differs from the latter by the different shape of both the pronotum and aedeagus (Figs 2, 3, 6–9).

TYPE MATERIAL. Holotype. Male, labelled: India, N Uttar Pradesh, Tapovan (ca 17 km SE of Gangotri), 4500 m, 26.vi.1996, leg. J. Kaláb. In the collection of J. Farkač, Praha. Paratypes. 4 males and 18 females, same data as holotype. In the collections of J. Farkač, Praha, W. Heinz, Schwannfeld, J. Kaláb, Jinačovice, J. Rolčík, Praha, R. Sciaky, Milano and A. Smetana, Ottawa.

ETYMOLOGY. The specific epithet is a Czech colloquial word "natruc", meaning "in spite of", in apposition. It refers to the reasons why the collector of the specimens went to India.



Figs 1–9. Pronotum of 1 – *Leistus* (*Evanoleistus*) *harpagon* sp. n., 2 – *L.* (*E.*) *natruc* sp. n., 3 – *L.* (*E.*) *nyingtri* sp. n. Aedeagus in dorsal and lateral view of 4, 5 – *L.* (*E.*) *harpagon* sp. n., 6, 7 – *L.* (*E.*) *natruc* sp. n., 8, 9 – *L.* (*E.*) *nyingtri* sp. n. Scale 1 mm (A: Figs 1–3, B: Figs 4–9)



Figs 10–12. General habitus of holotypes of: 10 – *Leistus* (*Evanoleistus*) *harpagon* sp. n.; 11 – *L.* (*E.*) *natruc* sp. n.; 12 – *L.* (*E.*) *nyingtri* sp. n.

***Leistus* (*Evanoleistus*) *nyingtri* sp. n.**

(Figs 3, 8, 9, 12)

DESCRIPTION (habitus of holotype as in Fig 12) Body length 9 5–10.1 (holotype 10 1 mm) Color piceous-black, tarsi, mandibles, maxillary appendages and antennae from fifth segment paler Antennal segment 1–4 paler, only at both ends Eyes prominent Gular setae situated on transverse carina Mandibles wide, relatively short, with short, sharp apex IA = 1 38–1 42

Pronotum (Fig 3) narrow, cordiform (IPm/b = 1 90–2 00) Lateral bead flat, wide, from about middle toward posterior angles dilated and elevated. Lateral margin just in front of posterior angles slightly sinuate, posterior angles rectangular Disc with distinctive middle line Basal impression irregularly punctate IPw/l = 1 28–1 36

Elytra broadly oval, punctation of striae distinct Lateral bead more distinct in anterior half, towards humeri elevated, humeri therefore appearing as having elevated seam Elytra highest at middle (lateral view) IE/P = 1 47–1 48, IEl/w = 1 62–1 71

Aedeagus (Figs 8, 9) Apex obtuse, in dorsal view very slightly curved downward to left side

AFFINITIES *Leistus* (*Evanoleistus*) *nyingtri* sp n differs from *L* (*E*) *thibetanus* Dvořak, 1994 by the different shape of the pronotum (Fig 3 and Dvořák, 1994 fig 9) It differs from the habitually similar *L* (*E*) *natruc* sp n by the different shape of both the pronotum and aedeagus (Figs 2, 3, 6–9)

TYPE MATERIAL Holotype Male, labelled Tibet (Nyingtri), Sarkyim-la (SW Seite), 4000–4100m, 27 /28 vi 1995, lgt [W] Heinz In the collection of W Heinz, Schwanfeld Paratypes Two males, same data as holotype In the collections of J Farkač, Praha and W Heinz, Schwanfeld

ETYMOLOGY The specific epithet is the name of the type locality, in apposition

***Leistus* (*Evanoleistus*) *championi* Andrewes, 1920**

Leistus championi Andrewes,1920 448, 1929 108, 1930 194, Banninger 1925 331, 333
Leistus (*Evanoleistus*) *championi* Perrault 1985a 15, Perrault 1985b 37, 47, *1986 127 1990 100–101*

DISTRIBUTION India (Uttar Pradesh: Kumaon, Garhwal), Nepal (Ode da Kakani, Surkhe, Janakpur, Dunda) (Perrault 1985b, 1986, 1990) First record to Meghalaya province

OTHER MATERIAL EXAMINED One male, labelled NE India, 25 40N 91 04E, W Meghalaya, Garo Hills, Nokrek Nat Park 1150m, 13 –22 12 1997, lgt S Murzin & V Siniaev, one male, labelled C Nepal, env Kathmandu, Rhanibam Mt R , Nagarjun Mt 15 iv –5 v 1996, leg P Udovichenko Both specimens are in the collection of J Farkac Praha

Acknowledgements

I thank all my colleagues who in any way contributed to the realization of this paper, particularly to Dr Aleš Smetana (Agriculture and Agri-Food Canada, Ottawa) for his help with English, Mgr Matuš Kocian (Research Institute of Crop Production, Praha) for his assistance with the preparation of the illustrations, Dipl Ing Pavel Moravek (Praha) for providing the photographs of the holotypes and my friend Dr David Kral (Charles University, Praha), for his support of my work

REFERENCES

ANDREWES H F 1920 Papers on oriental Carabidae *Ann Mag Natur Hist* 5 448

ANDREWES H E 1929 *The fauna of British India Coleoptera, Carabidae vol 1 Carabinae* London Taylor & Francis 431 pp

ANDREWES H E 1930 *Catalogue of indian insects* Part 18 Carabidae Calcutta, 194 pp

BANNINGER M 1925 Neunter Beitrag zur Kenntnis der Carabidae die Nebriini Gattung Leistus (Froehlig) *Entomol Mitt* **14** 329–343

DEUVE T 1985 Description d'un nouveau Leistus Froehlig du Nepal et notes sur le genre *Rev Fr Entomol (N S)* **7** 45–47

FARKAČ J 1995 Sixteen new species of Leistus from Asia (Coleoptera Carabidae Nebriini) *Acta Soc Zool Bohem* **59** 145–163

PERRAULT G -G 1985a Le genre Leistus Froehlig (Coleoptera – Carabidae – Nebriini) VI Le sous-genre Evanoleistus Jedlička (1) le groupe L nepalensis Jedlička *Bull Mens Soc Linn Lyon* **54** 13–24

PERRAULT G -G 1985b Le genre Leistus Froehlig (Coleoptera – Carabidae – Nebriini) VII Le sous-genre Evanoleistus Jedlička (2) le groupe L nepalensis Jedlička *Bull Mens Soc Linn Lyon* **54** 36–51

PERRAULT G -G 1986 Le genre Leistus Froehlig IX Complements a l' Etude du sous-genre Evanoleistus Jedlička (Coleoptera, Carabidae, Nebriini) *Rev Fr Entomol (N S)* **8** 127–133

PERRAULT G -G 1990 Le genre Leistus Froehlig XIV Supplement a la faune de l' Himalaya (Coleoptera, Carabidae) *Nouv Rev Entomol (N S)* **7** 99–104

WU CH F 1937 *Catalogus insectorum sinensium (Catalogue of Chinese insects)* III Peiping The Fan Memorial Institute of Biology, 256 pp

Acta Soc. Zool. Bohem. **62**: 207–216, 1998
ISSN 0862-5247

New taxonomic changes in the genus *Glipa* from the Oriental region and descriptions of three new species of the genus *Ophthalmoglipa* (Coleoptera: Mordellidae)

Jan HORÁK

K hádku 567, Dubeček, CZ-107 00 Praha 10 – Dubeč, Czech Republic

Received April 23, 1998, accepted September 24, 1998
Published October 30, 1998

Abstract. New species *Ophthalmoglipa maranoelai*, *O. bilyi* (Seram I.) and *O. iriana* (New Guinea) spp. n. are described and the key to the species of *Ophthalmoglipa* Franciscolo, 1965 from the Oriental and Australian regions is provided. *Mordella cinereonigra* Fairmaire, 1893 is transferred in the genus *Glipa* Leconte, 1859. Following new synonymies are proposed. *Glipa* (*Stenoglipa*) *rectefasciata* Pic, 1941 = *G. luteobasalis* Pic, 1941, *Glipa* (*Macroglipa*) *ogasawarensis* Kôno, 1928 = *G.* (*M.*) *salvazai* Pic, 1929, *Glipa* (*Macroglipa*) *cinereonigra* (Fairmaire, 1893) = *G. apicalis* Pic, 1922 and *Glipa* (*Macroglipa*) *separata* Pic, 1941 = *G. iriei* Takakuwa, 1977 synn. n. Species *Glipa nigronotata* Pic, 1941 is redecribed.

Taxonomy, Coleoptera, Mordellidae, new species, new combination, new synonymies, Oriental region, Australian region

INTRODUCTION

The present paper is the complement of my previous study on the taxonomy of the genus *Glipa* LeConte, 1859 (Horák 1994). Moreover, it contains descriptions of three new species of the genus *Ophthalmoglipa* Franciscolo, 1965, from Indonesia (Seram, Irian-Jaya), which represent a new well defined unit within the genus.

ACRONYMS

CHP – collection Jan Horák, Praha
MNHN – Muséum national d'Histoire naturelle, Paris

SYSTEMATICS

Glipa (*Stenoglipa*) *rectefasciata* Pic, 1941

Glipa rectefasciata Pic, 1941b: 3–4
Glipa (*Stenoglipa*) *rectefasciata*: Horák, 1994: 102.
Glipa luteobasalis Pic, 1941b: 4, **syn. n.**

GEOGRAPHIC DISTRIBUTION. Vietnam, Malaysia.

MATERIAL EXAMINED. 1 female, Cochinchine, Chuachan, 30. I. 1921, R. Vitalis de Salvaza, Lectotype (designated here) of *Glipa luteobasalis*, 1 female, Lao Kay, 9. 1912, Paralectotype (designated here) of *G. luteobasalis* (both MNHN). Further material (CHP): 2 males, Vietnam, Vinh phu prov., Tam dao, 27.5.–2.6.1986, Jan Horák leg.; 2 males, S Vietnam, 40 km NW of An Khe, Buon Luoi, 650–750 m, 14°10 N 108°30 E, 28.3.–12.4.1995, Pacholátko & Dembický leg., 1 female, West Malaysia, Perak, above Taiping city, Maxwell hill, 900–1000 m, 12–

16 1 1995, S. Becvar j & s leg., 1 female, Malaysia. Pahang, Cameron Highlands, 5 km S Tanah Rata, 1300 m, 28 7 1993, Schuh leg

Comments. Revision of the type material from the museum in Paris revealed that *Glipa luteobasalis* is but the opposite sex (female) of *G rectefasciata* The females can be separated from the closely related *G.* (*Stenoglipa*) *annulata* (Redtenbacher, 1868) according to a golden pubescence covering entire basal fourth of elytra.

Glipa (*Macroglipa*) *ogasawarensis* Kôno, 1928

Glipa ogasawarensis Kôno, 1928 32.
Glipa salvazai Pic, 1929 23, **syn. n.**

Geographic distribution. Japan, Vietnam.

Material examined 1 female, Cochinchina, P Condora, 11 8 1924, R Vitalis de Salvaza, Holotype of *Glipa salvazai* (MNHN), label "Holotype" added by myself. Further material (CHP) 1 female, N Vietnam, Vinh Phu distr, Tam Dao, 27 5 –2 6 1986, J Horák lgt, 1 male, 2 females, S Vietnam, Buon Luoi, 40 km NW of An Khe, 620–750 m, 14°10 N, 108°30 E, Pacholátko and Dembický lgt

Comments The species is closely related to *Glipa* (*Macroglipa*) *sauteri* Pic, 1911, from which it differs by the colour pattern of elytra. each elytron with one subhumeral spot and the apical fourth covered with black hairs and bordered with white ones, rest of elytra with golden brown pubescence. *Glipa salvazai* is quite identical with *G. ogasawarensis* and must be considered its junior synonym.

Glipa (*Macroglipa*) *cinereonigra* (Fairmaire, 1893) comb. n.

Mordella cinereonigra Fairmaire, 1893 302.
Glipa apicalis Pic, 1922 21, **syn. n.**
Glipa (*Macroglipa*) *apicalis*: Horák, 1994· 109–110.
Glipa (*Macroglipa*) *shibatai* Nakane, 1960. 17–19, **syn. by Horák, 1994.**

Geographic distribution. Japan, Vietnam, Laos, Thailand.

Material examined Langson (N. Vietnam), Ghrentra, 1 female, labelled "*Mordella cinereonigra* Fairm 1893" and with the red label "Type" by myself (Holotype of *M cinereonigra*, MNHN) Further material (CHP)· 1 female, N Vietnam, Tam Dao 900 m, 16 –23 5 1991, Jan Strnad leg, 1 female, N Vietnam (Tonkin), Tam Dao (pr Vinhphu), 2 –11.6.1985, Vit Kubáň leg ; 2 males, 1 female, N Vietnam, 75 km NW of Hanoi, Tam Dao, 900–1200 m, 21°27 N 105°39 E, 1 –8 6 1996, L. Dembický & P. Pacholátko leg.; 1 male, S Vietnam, 14 km SW of Bao Loc, 16 –29 5 1994, P Pacholátko & L Dembický leg, 2 males, Laos, Louang Namtha pr., Namtha to Muang Sing, 900–1200 m, 21°09 N 101°19 E, 5.–31.5.1997, Vít. Kubáň leg

Comments. The holotype of *Mordella cinereonigra* belongs to the genus *Glipa* and is quite identical with *G. apicalis* Pic, 1922, which must be considered its junior synonym.

Glipa (*Macroglipa*) *separata* Pic, 1941

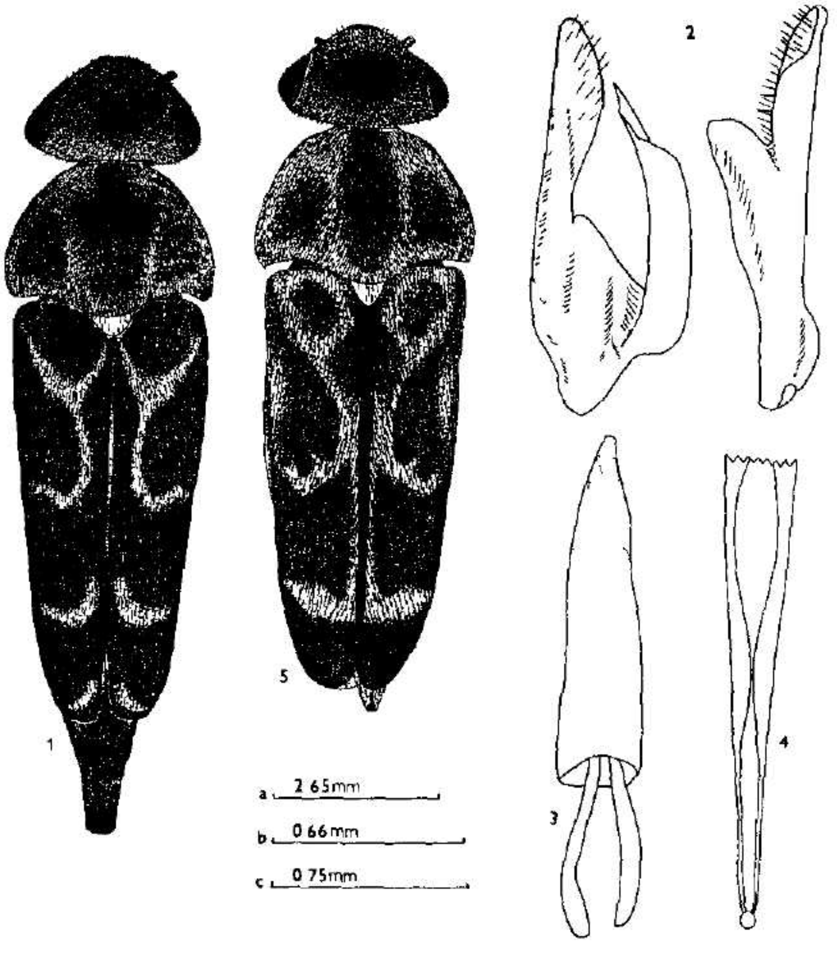
Glipa separata Pic, 1941b· 4
Glipa iriei Takakuwa, 1977 9–11, **syn. n.**

Geographic distribution. Japan, Vietnam, Thailand, Malaysia.

Material examined. Tonkin, Hoa Binh, 1 male labelled "*separata* n. sp", designated here as lectotype of *Glipa separata* Pic (MNHN); Tonkin, Hoa Binh, 1 female designated here as paralectotype of *G separata* (MNHN)

Further material (CHP) 1 male, N Vietnam, pr Vinh phu, Tam dao, 3 –11 6 1985, V Švihla leg , 2 females, Vietnam, Ha son binh pr , Hoa Binh, 4 –7 6 1986, Jan Horak leg , 1 male, N Vietnam, 75 km NW of Hanoi, Tam Dao, 900–1200 m, 21°27 N 105°39 E, 1 –8 6 1996, L Dembicky & P Pacholatko leg , 1 male N Vietnam, Sa Pa 11 –18 6 1990, A Olexa leg , 1 male, Thai, Namuang, 21 –26 5 1993, Pacholatko & Dembicky leg , 3 males, 2 females, S Thailand, Yala dist , Betong, Gunung Cang dun vill , 25 3 –22 4 1993, J *Horák* leg , 1 *female* Malaysia, Johor Endau riv , Selendang env , 29 4 –6 5 1993, Jenis & Strba leg

COMMENTS Very conspicuous middle-sized black species Pubescence black with characteristic white-grey pattern (Fig 1), in male on the head and pronotum golden-yellow The light pattern of



Figs 1–5 1–4 *Glipa (Macroglipa) separata* Pic, Lectotype, male 1 – general view, 2 – paramere, 3 – phallobasis, 4 – apex of penis 5 *G (M) nigronotata* Pic, Holotype, female 5 – general view Scale a –3, 4, b – 1, 5, c – 2

elytra less pronounced than in female, making up a very characteristic apical spot. Scutellum with brightly white pubescence. Very conspicuous is a short and strong, broadly truncate pygidium, Fore tibiae in male strongly curved inwards, at the base with long calf-shaped extension bearing long outstanding hairs. Fore tarsi very short, the first tarsomere as long as the three following ones combined; those are, however, somewhat wider. The fourth tarsomere deeply bilobed with truncate onychium Hind tibia besides an apical ridge with one distinct dorsal ridge, hind tarsi without ridges. Outer terminal spur of hind tibia reaching slightly more than one third of the length of the inner one, both spurs black-brown.

Male genitalia as figured (Figs 2,3,4).

Length (tips of mandibles to tips of elytra) 9–11.1 mm, to the tip of pygidium 10.8–11.9 mm.

This species is known also from southern Japan (Okinawa and Ryukyu Is.). It was mentioned for the first time as *Glipa* sp. by Takakuwa (1976) and subsequently described as *G. iriei* Takakuwa, 1977. This species is, however, quite identical with *G. separata* and must be considered its junior synonym.

Glipa (*Macroglipa*) *nigronotata* Pic, 1941

Glipa nigronotata Pic, 1941a: 10.

GEOGRAPHIC DISTRIBUTION. Vietnam.

MATERIAL EXAMINED Hoa Binh, 1 female labelled "*nigronotata* n. sp." and subsequently labelled "Holotype" by myself (holotype , MNHN), Additional material. N Vietnam, Shon La prov, Moc Tjau, 14. 5. 1991, J. Strnad lgt , 1 female (CHP); N Vietnam, Cuc Phuong, 2.–11. 5. 1991, J. Strnad lgt , 1 female (CHP).

COMMENTS. More detailed classification of this very interesting species is impossible at present. It belongs to the complex of species related to *Glipa* (Macroglipa) *brevicauda* Blair, 1931, which includes many closely related species . Thorough revision of this complex, based on the relevant type material, is badly needed. The original description is complemented here with the illustration of the habitus with characteristic colour pattern of dorsal surface (Fig. 5).

Key to species of *Ophthalmoglipa* from the Oriental and Australian regions

1 (2) Tips of elytra, base of pygidium and spots on ventral surface covered with golden-yellow pubescence Australia (Queensland) .. .. *O elongatula* (Mac Leay, 1872)

2 (1) Tips of elytra, base of pygidium and spots on ventral surface covered with white pubescence

3 (4) Golden yellow pubescence in basal portion of each elytron covers a mediolongitudinal spot ending at one third of the elytral length Central and eastern New Guinea. . .. . *O. australis* Franciscolo, 1965

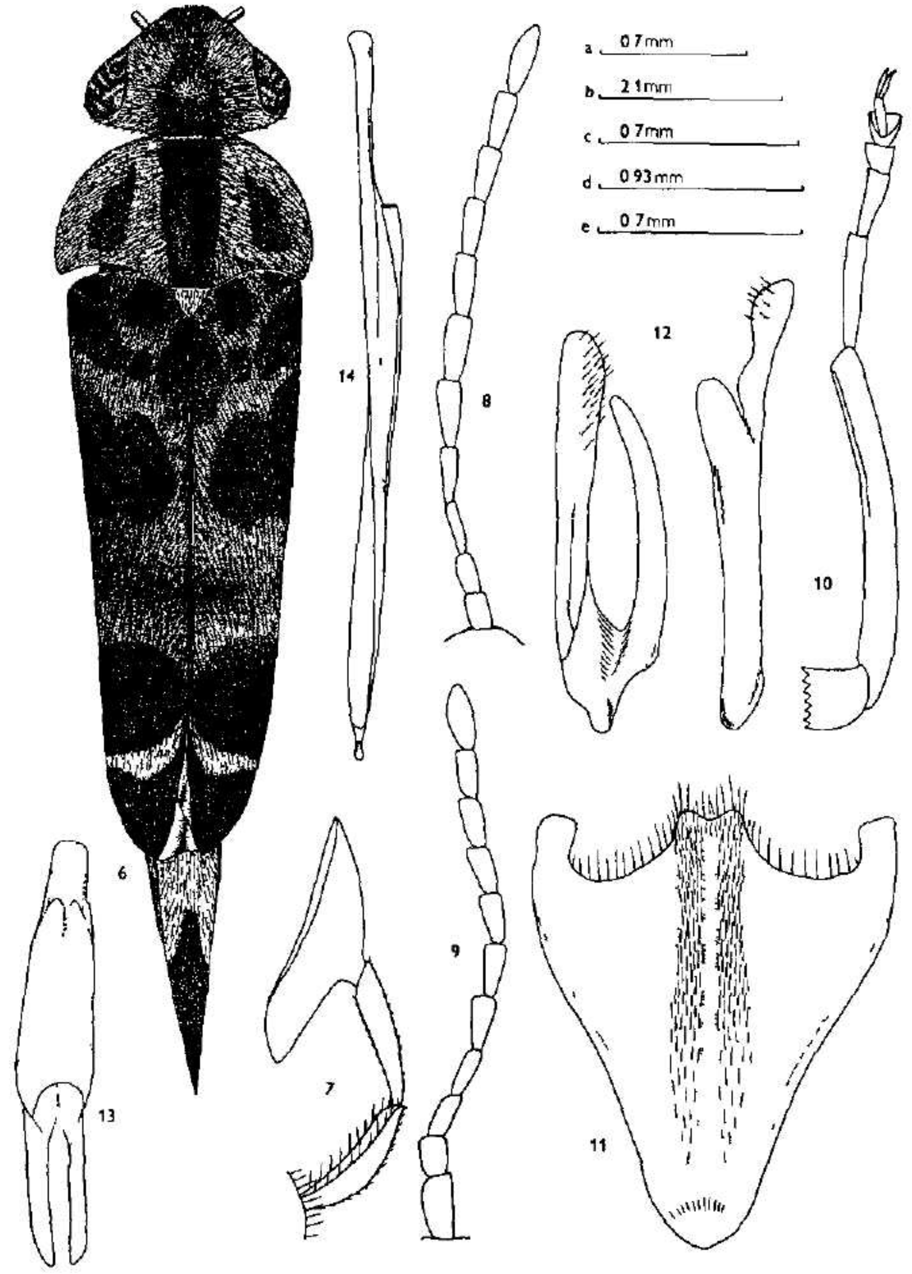
4 (3) Golden yellow pubescence covers entire basal third of each elytron, surrounding two to three spots of black hairs round postscutellar spot (missing in *O bilyi* sp n), one spot at basal corner of scutellum and a somewhat elongate and vaguely limited humeral spot

5 (6) Humeral golden-yellow pubescence narrowly interconnected along suture with median transverse bar Pubescence of head and pronotum either golden-yellow (male) or silvery (female) Fore tibiae in male strongly curved inwards. Urosternite 8 very broad, projecting into long processes laterally. Maluku Is (Seram). .... *O. maranoelai* sp n

6 (5) Humeral golden-yellow pubescence separated from the median transverse bar Fore tibiae in male only weakly curved inwards.

7 (8) Round black postscutellar spot surrounded by golden-yellow pubescence developed Pubescence of head and pronotum in male golden yellow Urosternite 8 projecting into two long lateral processes apically, its apical portion consequently with two deep arcuate emaeginations separated by median protuberance New Guinea (Irian-Jaya) .... *O iriana* sp. n

8 (7) Round postscutellar black spot absent. Head and pronotum in male with silvery pubescence. Urosternite 8 truncate apically with median pubescent protuberance. Maluku Is (Seram). .. .. *O bilyi* sp. n.



Figs 6-14 *Ophthalmoglipa maranoelai* sp n, Holotype, male 6 – general view, 7 – maxillary palpus, 8 – antenna 9 – antenna (Allotype, female), 10 – anterior tibia and tarsus, 11 – 8° internal sternite, 12 paramere, 13 – phallobasis 14 – penis Scale a 11, b – 6 c – 7, d – 8, 9, 10, 13, 14, e 12

Ophthalmoglipa maranoelai sp. n.

(Figs 6–14)

TYPE MATERIAL Holotype, male, Maluku Is , Seram, Solea, 12 km of Wahai, 17 1–6 2 1997, J Horak lgt (CHP) Allotype female, the same data (CHP) Paratypes 19 spec , the same data as Holotype, 1 female, ditto but S Bily lgt (CHP, MNHN and coll I Jeniš, Naklo, Czech Republic)

DESCRIPTION Male Slender (Fig 6), from basal third of pronotum gradually narrowed posteriorly Body black, postclypeus and labrum brown, anteclypeus yellow, galea golden-brown Entire maxillary palpi yellow, terminal segment somewhat infuscate Antennomeres 1–2 yellow-brown, 3–4 black-brown distally, 5–6 with only bases yellowish Fore femora brown, fore tibiae black-brown with lighter base, the first segment of fore tarsi with yellow-red base, mid femora brown, bases of the first and second segments of mid tarsi red-brown, terminal spurs of hind tibiae black-brown Pubescence tricoloured basic pubescence black with golden pattern, which passes into golden-red in median portion of elytra, praeapical spot on elytra and ventral surface (excluding sides of abdominal sterna, whole hypopygium and two distal thirds of pygidium) covered with silvery hairs

Head flatly convex, wider than long (as 15 11 3), finely and densely punctate Eyes broadly oval, only indistinctly narrowed towards antennal insertions, finely facetted and glabrous Temples not developed, only temporal angle on ventral surface developed Maxillary palpi long, as figured (Fig 7) Antennae long, filiform, for proportions of antennomeres see Fig 8

Pronotum flatly convex, much wider than long (as 18 7 13) Basal lobe semicircular, occupying somewhat less than one third of the width of basal margin Anterior margin in dorsal view semicircular with feebly marked anterior angles, without collar-shaped projection Lateral margins in lateral view almost straight, posterior angles obtuse Dorsal surface with fine rasp-like puncturation

Scutellum subtriangular with rounded apex

Elytra distinctly narrower than pronotum, from humeri gradually narrowed posteriorly (more strongly so in apical fifth), separately rounded at apex, 2 4 times longer than their combined width Punctures coarse and dense, rasp-like

Pygidium narrowly conical, twice as long as hypopygium, with acute apex and with sharp mediolongitudinal dorsal carina in apical half

Fore tibiae (Fig 10) strongly curved inwards, without a calf-shaped basal extension and with uniform pubescence Fore tarsi distinctly shorter than fore tibiae (as 7 8 9 2) and gradually dilated towards the fourth segment Tarsomere 1 shorter than the following ones combined (as 3 4 2), tarsomere 4 deeply bilobed, ventrally with truncate onychium, tarsomere 5 only a little more than twice as long as 4 Mid tibiae only a little longer than mid tarsi (as 12 11) Hind tibiae with short apical ridge reaching nearly one fourth of the tibia width and one little distinct dorsal ridge developed as a series of granules The first hind tarsomere also with an indistinct series of granules, following tarsomeres without ridges or granules Outer terminal spur of hind tibia by almost one fifth shorter than the inner one

Male genitalia as figured (Figs 11,12,13,14)

Length from tips of mandibles to tips of elytra 9 4 mm, to the tip of pygidium 12 5 mm

Female Body stouter, antennae shorter (Fig 9) and fore tibiae straight

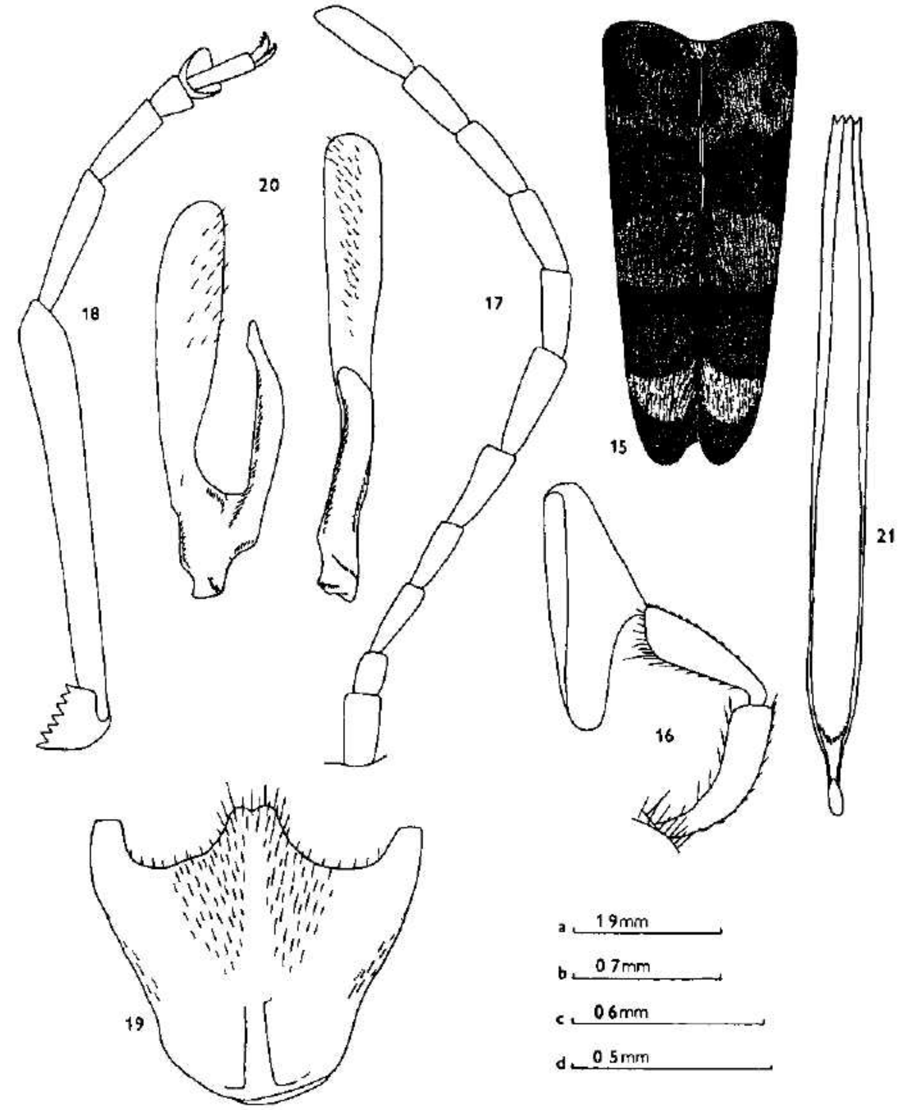
VARIATION Habitus rather constant Pubescence of the head and pronotum (mostly in females) sometimes silvery instead of golden Shape of pygidium variable, broadly to narrowly conical, in both sexes Length of body from the tips of mandibles to those of elytra 8 7–11 0 mm, to the tip of pygidium 11 2–13 8 mm

DIFFERENTIAL DIAGNOSIS For the differentional diagnosis see the above key

ETYMOLOGY Dedicated to Mr E Maranoela, director of the National Parc Manusella in Wahai (Seram)

Ophthalmoglipa iriana sp. n.
(Figs 15–21)

TYPE MATERIAL Holotype, male, New Guinea, Irian Jaya, Nabire cave, WanPP c r, 1994, Pljutsch lgt (CHP)



Figs 15–21 *Ophthalmoglipa iriana* sp n, Holotype, male 15 – elytra, 16 – maxillary palpus, 17 – antenna, 18 – anterior tibia and tarsus, 19 – 8° internal sternite, 20 – paramere, 21 – apex of penis Scale a – 15, b – 19, c – 16 17 18 21, d – 20

Description. Male. Slender, from basal third of pronotum gradually narrowed posteriorly. Black, postclypeus and anterior margin of labrum dark brown and anteclypeus yellow. Maxillary palpi yellow. Antennomeres 1 to 4 completely, 5 to 7 only at base brown. Fore femora brown, fore tibiae and tarsi black-brown. Bases of mid femora and of the first segment of mid tarsi brown. Terminal spurs of hind tibiae black-brown. Pubescence tricoloured: basic pubescence black with golden pattern, broad transverse bar behind the midlength of elytra golden-red, silvery pubescence covering the praeapical spot on elytra (Fig. 15), legs and ventral surface excluding apical margins of abdominal sterna, entire hypopygium and two apical thirds of pygidium.

Head flatly convex, wider than long (as 13 : 10), finely and densely punctate. Eyes broadly oval, not narrowed towards antennal insertions, very finely facetted and quite glabrous. Temples not developed except for distinct apical angle on ventral surface. Maxillary palpi long and as figured (Fig. 16). Antennae long, filiform, for the shape and proportions of antennomeres see Fig 17.

Pronotum feebly convex, much wider than long (as 15.4 : 10). Posterior lobe broadly semicircular, occupying one third of the width of basal margin. Anterior margin (dorsal view) semicircular with marked anterior angles and without collar-shaped projection. Lateral margins in lateral view moderately arcuate, posterior angles broadly obtuse. Surface with dense rasp-like puncturation.

Scutellum subtriangular with rounded apex.

Elytra distinctly narrower than pronotum, 2.4 times longer than their combined width at humeri, from there gradually narrowed posteriorly, separately rounded at apex. Puncturation of elytra coarse and dense, rasp-like.

Pygidium 2.3 times longer than hypopygium, narrowly conical with acute apex, distinctly and sharply longitudinally carinate in apical half.

Fore tibiae (Fig. 18) only gently curved inwards, without a calf-shaped basal extension and with uniform pubescence. Fore tarsi shorter than fore tibiae (as 6 : 8), only feebly dilated towards the fourth segment; tarsomere 1 shorter than the following ones combined (as 3 : 4), tarsomere 4 deeply bilobed, with truncate onychium ventrally, tarsomere 5 a little more than twice as long as 4. Mid tibiae longer than mid tarsi (as 10 : 8.5). Hind tibiae with short apical ridge reaching nearly one fourth of the tibia width and with one little distinct dorsal ridge developed as a series of granules. Hind tarsi without ridges or granules. Inner terminal spur of hind tibia slightly longer than the outer one.

Male genitalia as figured (Figs 19–21).

Length from tips of mandibles to tips of elytra 8.2 mm, to the tip of pygidiium 10.5 mm.

Female unknown.

Differential diagnosis. For the differentional diagnosis see the above key.

Etymology. Name derived from the name of the Indonesian part of the New Guinea, Irian-Jaya.

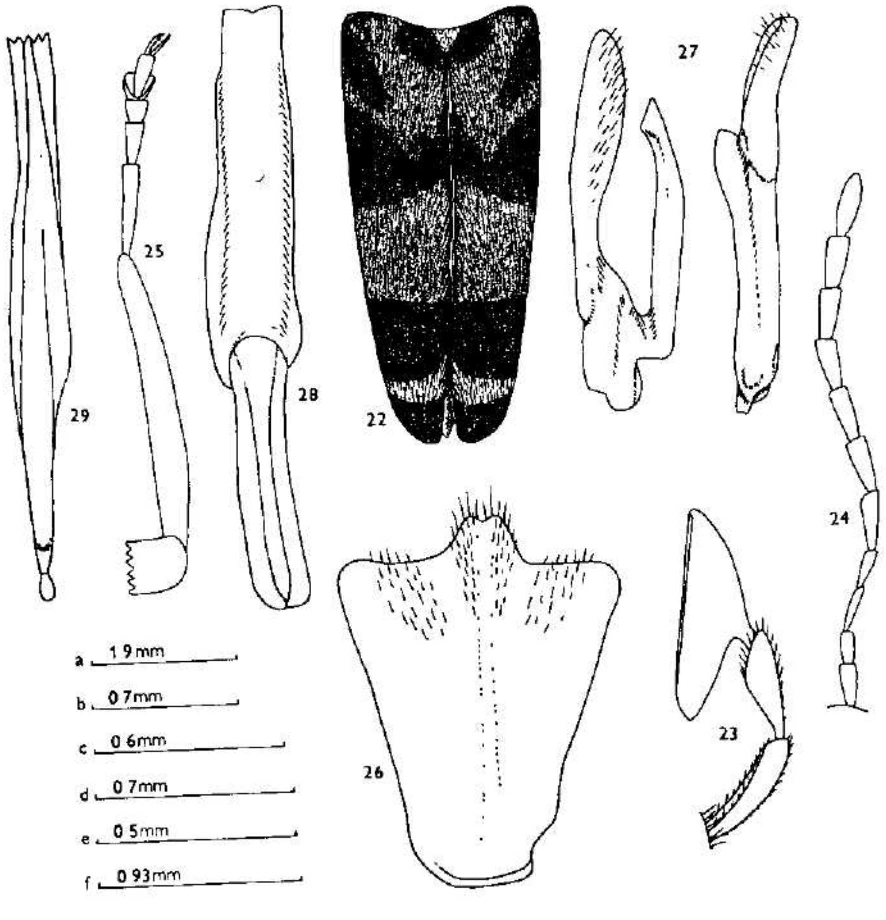
Ophthalmoglipa bilyi sp. n.

(Figs 22–29)

Type material. Holotype, male, Maluku Is., Seram, Solea, 12 km of Wahai, 17. 1.–6. 2. 1997, J. Horák lgt. (CHP).

Description. Male. Narrow, from basal third of pronotum gradually narrowed posteriorly. Black, ante- and postclypeus yellow, labrum black-brown with red-brown anterior margin. Galeae yellow-brown, maxillary palpi yellow-brown with infuscate basal posrtion of the fourth segment. Antennomeres 1 to 4 as well as basal postions of antennomeres 5 to 10 red-brown. Fore tibiae black, at both proximal and distal ends red brown. Fore tarsi black, only the fifth segment and onychium of the fourth segment red-brown. Dorsal and apical portions of mid femora red-brown, also the base of the first segment, onychium of the fourth segment and the entire fifth segment of mid tarsi red-brown.

Terminal spurs of hind tibiae black-brown. Pubescence tricoloured: basic pubescence silvery-white, golden pubescence covers base of elytra and transverse bar behind the midlength of elytra (Fig. 22); three spots on pronotum, two spots at the base of each elytron, transverse bar behind the golden elytral base and another bar before the apical silvery spot, apical margins of abdominal sterna, entire hypopygium and apical third of pygidium covered with black hairs. Legs with silvery pubescence.



Figs 22–29 ***Ophthalmoglipa bilyi*** **sp. n., Holotype, male.** 22 – elytra, 23 – maxillary palpus, 24 – antenna; 25 – anterior tibia and tarsus; 26 – 8^{c} internal sternite; 27 – paramere; 28 – phallobasis; 29 – apex of penis. Scale: a – 22, b – 26, c – 28, 29; d – 23; e – 27, f – 24, 25.

Head flatly convex, much wider than long (as 12 : 9), finely and densely punctate. Eyes broadly oval, gently narrowed towards antennal insertions, very finely facetted, glabrous. Temples not developed except for feebly marked temporal angle on ventral surface.Maxillary palpi long, terminal segment very short and extremely broad with both lateral margins equally long (Fig. 23). Antennae long, filiform, shape and proportions of antennomeres as figured (Fig. 24).

Pronotum flatly convex, much wider than long (as 16 : 10.5). Posterior lobe semicircular, occupying less than one third of the width of basal margin. Anterior margin semicircular, without collar-shaped projection. Lateral margins in lateral view moderately arcuate, posterior angles broadly obtuse. Surface of pronotum with dense and rather fine rasp-like puncturation.

Scutellum triangular.

Elytra narrower than pronotum, 2.4 times longer than their combined width, gradually narrowed posteriorly, separately rounded at apex, with coarse and dense rasp-like puncturation.

Pygidium elongate, conical, twice as long as hypopygium, with acute apex, distinctly longitudinally carinate in two posterior thirds.

Fore tibiae moderately curved inwards (Fig. 25), without calf-shaped basal extension and with uniform pubescence. Fore tarsi shorter than fore tibiae (as 6 : 9), gradually dilated towards the fourth segment, first segment as long as the following ones combined, the fourth one deeply bilobed with truncate onychium ventrally; the fifth segment twice as long as the fourth one. Mid tibiae a little longer than mid tarsi (as 10 . 9). Hind tibiae with short apical ridge reaching one third of the tibia width and with indistinct dorsal ridge, developed as a series of discrete granules. The first segment of hind tarsi with the series of four granules dorsally, following segments smooth. Terminal spurs of hind tibia of approximately equal length.

Male genitalia as figured (Figs 26–29).

Length from tips of mandibles to tips of elytra 8.8 mm, to the tip of pygidium 11.4 mm.

Female unknown.

Differential diagnosis. For the differentional diagnosis see the above key. Very peculiar is the shape of the eighth sternite, which is long, without strongly prominent lateral processes apically (Fig. 26).

Etymology. Dedicated to my friend and travelling partner, Svatopluk Bílý, who accompanied me during the collecting trip to Seram in 1997.

Acknowledgements

I wish to express my thanks to Dr Claude Girard (Muséum national d'Histoire naturelle, Paris), who enabled me to study the Pic's and Fairmaire's types in his charge.

REFERENCES

FAIRMAIRE L 1893: Note sur quelques Coléoptères des environs de Lang-Son *Mém Soc Entomol Belg* **37** 287–302

FRANCISCOLO M 1965 La Neoglipa e generi vicini della Nuova Guinea *Ann Mus Civ Stor Natur Genova* **65** 325–357

HORAK J 1994 Description of Glipa (Macroglipa) thoracica sp. n and revision of some species of the genus Glipa Leconte from the Oriental region. *Fol Heyrovskyana* **2** 101–110

KÔNO H 1928. Die Mordelliden Japans (Col) *Trans Sapporo Natur Histor. Soc* **10**· 31–46.

PIC M 1929. Nouveautés diverses. *Mél Exot -Entomol* **54**: 19–28.

PIC M 1941a "L Echange" *Revue Linéenne, Numero special, Opuscula martialis* (V) **1941**. 1–16.

PIC M 1941b "L Échange". *Revue Linéenne Numero special Opuscula martialis* (III) **1941** 3–10.

TAKAKUWA M 1976. List of the tribe Mordellini from the Yaeyma Islands (Japan). *Elytra* **3**: 15–18.

TAKAKUWA M 1977 A new Species of the Genus Glipa LeConte from the Ryukyu Islands (Mordellidae). *Elytra* **5** 9–11.

Acta Soc. Zool. Bohem. **62**: 217–225, 1998
ISSN 0862–5247

A new gall midge species *Asphondylia anatolica* sp. n. (Diptera: Cecidomyiidae) causing galls on *Astragalus lagurus* (Fabaceae) in Turkey

Marcela SKUHRAVA[1] & Halit ÇAM[2]

[1]Czech Zoological Society, Viničná 7, CZ–128 00 Praha 2, Czech Republic
[2]Gaziosmanpasa Universiteşi, Ziraat Fakultesi, Bitki Koruma Bolumu, 60030 Tokat, Turkey

Received August 10, 1998; accepted September 24, 1998
Published October 30, 1998

Abstract. *Asphondylia anatolica* sp. n. is described from specimens reared from large galls on stems of *Astragalus lagurus* Willdenow, 1794 (Fabaceae) found in a stony desert area in northern Turkey. Male, female, pupa and gall are described and morphological characters are illustrated. Life history and occurrence are given. Taxonomical problems of the genus *Asphondylia* Loew, 1850 are discussed.

Taxonomy, galls, Diptera, Cecidomyiidae, *Asphondylia*, Palaearctic region

INTRODUCTION

Conspicuous, peculiar and very large galls on the stems of *Astragalus lagurus* Willdenow, 1794 (Fabaceae [= Leguminosae, = Viciaceae]) were found by H. Çam during his investigations of insect fauna associated with various host plants growing in a stony desert area at Taşlıçiftlik (Stony Farm) in northern Turkey.

He reared several adults from galls on *A. lagurus* and sent them for determination to M. Skuhrava. She examined specimens and concluded that it is an undescribed species of the genus *Asphondylia* Loew, 1850.

The gall midge fauna of Turkey is not too abundant and includes as far as it is known only 34 gall midge species (Skuhravá et al. 1984, Skuhravá 1986). The discovery of a new species is, therefore, very interesting.

From the point of view of the biogeographical classification, the territory of Turkey, where the galls of the new gall midge species were found, is included in the Anatolian-Iranian Desert Biogeographic Province (Udvardy 1975). The country of northern Turkey belongs to the area where the prevailing climate is cold and semi-arid. Steppes, wooded or treeless, are characteristic of the flora of the Asian semi-deserts with cold winters, that is the Irano-Turanian province. The treeless steppes are covered with *Astragalo-Brometea*, *Onobrycho-Thymetalia leucostomi*-assotiations (Noirfalise 1987).

Astragalus Linnaeus, 1753 includes annual and perennial herbs or small shrubs with about 1800 species occurring in the world, mainly in the area of Central Asia. About 140 species occur in Europe. *Astragalus lagurus* is a dwarf cushion-forming shrub with short stems and pale yellow or pink flowers, turning purplish with age. It occurs in steppe, mountains, hilly pastures in north-west Iran, Armenia and Georgia, at altitudes from 1200 to 2890 m a. s. l. *Atragalus lagurus* is an Iranian-Turkish floral geoelement (Tutin et al. 1968, Davis 1970).

Asphondylia is a large, cosmopolitan genus including about 200 described species of which 51 species were described from the Palaearctic region (Skuhravá 1986). Only two species, viz. *Asphondylia verbasci* (Vallot, 1827) causing galls on flowers of various species of *Verbascum* Linnaeus, 1753 and *Asphondylia gennadii* (Marchal, 1904) (syn. *A capsici* Barnes, 1932), causing galls on fruits of *Ceratonia siliqua* Linnaeus, 1753 and *Capsicum annuum* Linnaeus, 1753, are known to occur in the territory of Turkey.

Although knowledge of the occurrence and distribution of plant galls in Asia is on a relatively high level, having been summarized by Houard (1922–1923), only a single finding of galls on *Astragalus* sp., which are similar to galls found by H. Çam, is given in this book with reference to a paper of Rübsaamen (Houard 1922–1923). Rübsaamen (1902) reported about galls collected by J. Bornmüller in the Orient and gave a description of the gall on *Astragalus* sp. (sectio *Tragacantha* Bunge, 1869), described and illustrated the pupa which he found inside this gall. Galls were collected at Mt. Hermon (Antilibanon) in Syria at an altitude of 2600 m a. s. l. in June 1897. Rübsaamen (1902) did not name this species because he did not know adults.

Unfortunately, the material referring to the species of *Asphondylia* sp. causing galls on *Astragalus* sp. in Syria has not been found in Rübsaamen's collection of gall midges which is deposited and preserved now in the Museum of Natural History, Humboldt University, Berlin, Germany.

MATERIAL AND METHODS

Galls on *Astragalus lagurus* and the reared adults from these galls were prepared and preserved dry. It was necessary for microscopic examination of morphological characters to transfer adults which were dry and glued on card points onto permanent slides

Dry adults on card points on insect pins were enclosed for 24 hours in a glass containing on its bottom a layer of clean sand which was entirely saturated by water and covered with a filter paper This container was hermetically closed with a lid Then the adults were carefully separated from the glue and successively transferred in small glasses with 75%, 95%, 100% alcohol and in the end in xylol, in each liquid at least for one hour. After this procedure, adults were mounted on microscope slides with Canada balsam as a medium, most of them in natural lateral position Head and male terminalia of some specimens were disconnected from the body and placed in dorsoventral position under separate cover glasses but on the same slide with the rest of the gall midge body

Asphondylia anatolica sp. n.

(Figs 1–16, 19)

Type material Holotype. male, northern Turkey, Taşlıçiftlik near Tokat, 12.vi 1993, leg. Halit Çam, slide number Nr 7106, from galls on *Astragalus lagurus* Willd Paratypes. two males and two females, same data; all in the *collection of M Skuhravá in the National Museum, Praha, Czech Republic*

Additional material. 4 pupae, several pupal skins, 13 adults, emerged 4 –7.vi.1997, same locality.

Description. Male (Figs 1–8). Body size: 3.8 mm long; wing length 4.5 mm, wing width: 1.7 mm. Head, thorax and abdomen dark brown coloured. Head of normal size and position; occiput in lateral view prominent. Head with large holoptic eyes; eye bridge 12 ommatidia broad medially. Eyes with many circular ommatidia. Mouthparts reduced. Maxillary palps three segmented, all segments covered with relatively long setae. First segment very short, third segment about twice longer than the second segment. Palpiger absent. Frontoclypeus with a group of thin, 120–130 µm long setae.

Antennae 2 + 12 segmented, flagellomeres cylindrical with very short stems. Scapus obconical, pedicellus small, ovoid and subglobular, covered sparsely with setae; first and second flagellomeres without stems. Each flagellomere covered with tortuous adpressed circumfila forming net and with many thin setae. Terminal flagellomere prolonged.

Wings relatively large and broad with prominent alar lobe. Costa interrupted at the point of junction with R_5; subcosta visible only in the basal part. R_1 reaches to the middle of the anterior wing margin. The field between costa and R_1 is opaque. R_5 straight and joining costa at the wing apex. Median fold is present. Cu is forked. Wings covered with microtrichia and with hairs.

Legs long, covered with hairs and scales. Claws simple on all legs, strongly sclerotized, black, bent near midlength. Empodia as long as claws or a little longer than claws.

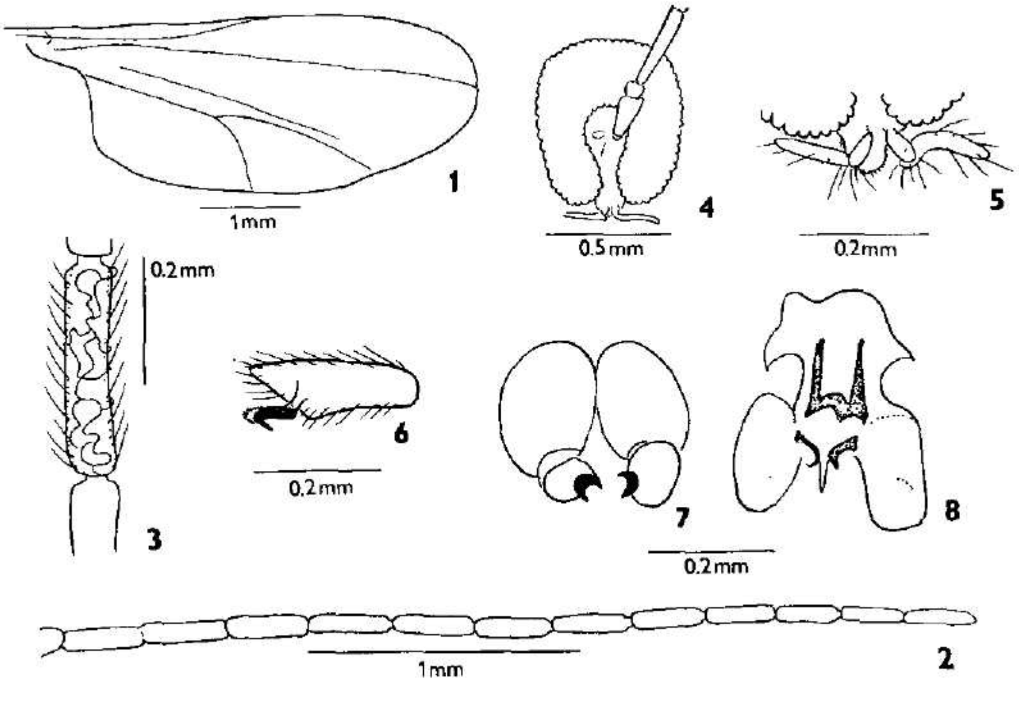
Male terminalia relatively small. Gonocoxites thick and ovoid, fused mediobasally; gonostyli also ovoid, inserted dorsally on gonocoxites, with bidentate and strongly sclerotized claw apically. Cerci and hypoproct small and bilobed. Aedeagus short, pointed, at the base with hook-shaped parameres.

FEMALE (Figs 9–14). Body size: 3.6 mm long, wing length 4.8 mm, wing width 1.8 mm. Antennae 2+12 segmented, flagellomeres cylindrical, nearly without stems, distal three segments strongly shortened, the terminal segment globular. Flagellomeres densely covered with microtrichia, with many sensorial hollows and hairs and with a sensorial thread forming usually two rings which are connected by a commisure.

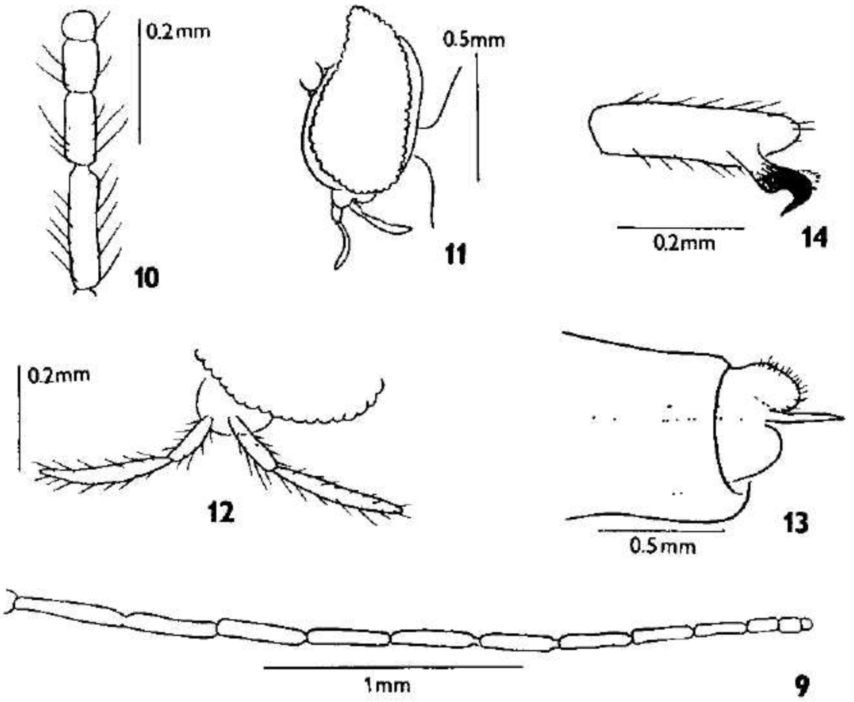
Ovipositor basally with two dorsal lobes; terminal part aciculate.

Other morphological characters as in the male.

PUPA (Figs 15–16). Body is 4.5–5.2 mm long, dark brown coloured; head part, sheaths of wings, antennae and legs black. Bases of antennal sheaths with a pair of large, black, strongly sclerotized antennal horns. Horns are acutely pointed, with finely denticulate inner margin. A pair of cephalic setae 70–80 mm long. Facial part with upper and lower frontal horns situated medially. Upper frontal



Figs 1–8. *Asphondylia anatolica* sp. n., male. 1 – wing; 2 – antenna total; 3 – 5th flagellomere; 4 – head in frontal view; 5 – mouthparts with palpen; 6 – 5th tarsomere with claw and empodium, 7 – hypopygium (dorsal part); 8 – basal part of hypopygium showing the aedeagus.



Figs 9–14. *Asphondylia anatolica* sp. n., female. 9 – antenna, 10 – terminal flagellomeres; 11 – head in a lateral view; 12 – mouthparts with palpen; 13 – end part of female abdomen with ovipositor; 14 – 5th tarsomere with claw and empodium

horn is formed of two bent, strongly sclerotized spinae which are placed on one shared base. Lower frontal horn consists of two large, strongly sclerotized protuberances situated laterally and one small situated medially (this is in some specimens invisible). Prothoracic spiracle 200 µm long, tapering from base to the tip.

Each abdominal segment, except first and terminal ones, is dorsally covered with spinae. The spinae in the anterior part of segments are smaller and irregularly situated, successively they are larger and in the posterior part of segments there is a transverse row of 20–30 large spines, each 35–40 µm long.

Terminal segment is anteriorly also covered with small spinae and apically has a group of two or three large spinae, 60 µm long, which are situated on both side, and with 6–8 smaller, 30 µm long spinae.

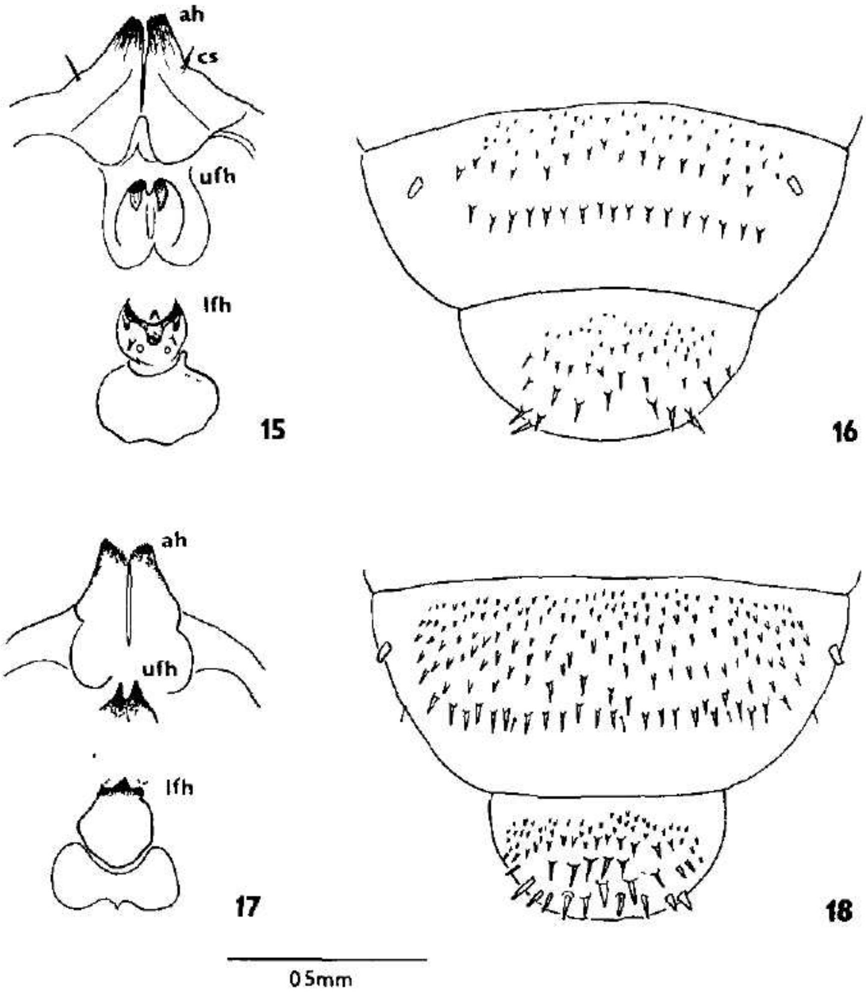
Ventral part of abdominal segments is quite without spinae; the skin is formed of small, round, close-fitting plates.

DIFFERENTIAL DIAGNOSIS. Adults of *Asphondylia anatolica* sp. n. are morphologically very similar to adults of *A. sarothamni* Loew, 1850, the type species of the genus *Asphondylia* Loew, 1850. The pupa of *A. anatolica* sp. n. differs from the pupa of *A. sarothamni* in the shape of the upper and lower frontal horns and by the number, size and placement of spines on dorsal part of the 7th and 8th abdominal segments (Figs 17–18). *A. anatolica* sp. n. differs also in the shape of the upper and lower frontal horns from *A ervi* Rubsaamen, 1896, which was described and figured by Yukawa (1985)

NAME DERIVATION The new gall midges species is named after Anatolia, Asian part of the territory of Turkey, where the type locality lies

HOST PLANT *Astragalus lagurus* Wildenow, 1794 (Fabaceae)

GALL (Fig 19) The gall of *Asphondylia anatolica* sp n. is large, globular, about 25 mm in diameter and is situated at the tip of the woody branch of *Astragalus lagurus*. The surface of the gall is



Figs 15–18 15–16 *Asphondylia anatolica* sp n , pupa 15 – head part (ventral view) with a pair of antennal horns (ah) a pair of cephalic setae (cs), upper frontal horn (ufh) and lower frontal horn (lfh), 16 – dorsal part of 7th and 8th abdominal segment, 17–18 *Asphondylia sarothamni* Loew, pupa 17 – head part (ventral view), 18 – dorsal part of 7th and 8th abdominal segment

formed by many very small, narrow leaves which are densely covered with hairs. The gall is composed from about 10–15 smaller galls each of them with one chamber inside covered with mycelium. Only one larva develop in one chamber. Also the pupation takes place in the gall.

Galls of *A. anatolica* sp. n. were found in northern Turkey, at the locality Taşliçiftlik (Stony farm), about 7 km westwards from the town Tokat, in the area situated at 40°20' north latitude, 36°35' east longitude and at an altitude of about 630 m a. s. l. Annual average temperature is 12.4 °C, the annual mean precipitation 438.4 mm and the relative humidity 64% (Anonymous 1994). The examined locality is on the north side of the valley of the river Yesilirmak (Green River) and is formed by stony and rocky places with only poor plants. The soil structure is stony calcareous ground. Plant cover is formed mainly by tragacanth steppe.

The area of about 1000 quadrat meters has been examined in 1993 and only 156 specimens of *Astragalus lagurus* were found. Only eleven of these were attacked by *Asphondylia anatolica* the larvae of which cause terminal stem galls. Taşliçiftlik is the only one place where the galls of *Asphondylia anatolica* sp. n. were found. From that fact it seems that the galls of *Asphondylia anatolica* sp. n. are very rare.

Life history

Larvae cause large terminal stem galls on *Astragalus lagurus*. About 10–15 larvae develop in one complex gall. Each larva form one gall the wall of which is inside covered with mycelium. Pupation takes place in the gall. In 1993, the adults emerged between 12th to 16th June and in 1997 between 4th to 7th June. Only five adults (two females and three males) were reared from one gall. Probably only one generation develops a year. It is not quite clear where females lay their eggs; probably on the tip of the branch.

Distribution

Asphondylia anatolica sp. n. seems to be a very rare gall midge species. Although its host plant, *Astragalus lagurus*, occupies a relatively large area having been an Iranian-Turkish element, galls of *A. anatolica* sp. n. were found only in a small area in stony desert in the northern part of Turkey (Fig. 20). It is possible that galls found by Bornmüller on *Astragalus* sp. at Hermon in Syria in 1897 (Rübsaamen 1902) which are similar to galls of *A. anatolica* sp. n. were caused by the same gall midge species. It was not possible to solve the identity of these two species because the original material of *Asphondylia* sp. from Syria is lost.

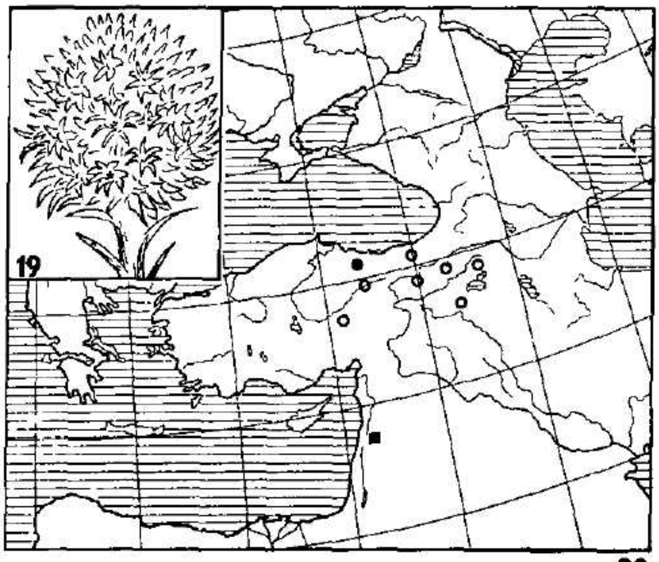
DISCUSSION

From the taxonomical point of view, the genus *Asphondylia* is very difficult for elaboration. Adults are very similar one to another in morphological characters and at present there are no keys for determination of species. Some dissimilarities in morphological characters may be found in the larval stage – in the shape of the spatula sternalis (the sclerotized cuticular organ on the ventral side of the prothoracic segment) and in the pupal stage in various structures on the head and dorsal parts of abdominal segments.

Some difficulties in the determination of species belonging to the genus *Asphondylia* are due to the present situation in this family. Many gall midge species have been described from adults in the past but – from the point of view of present taxonomy – very unsufficiently, some species have been described based on the larva only and some species were described even on the gall only. The morphological characters of adults, pupae and larvae belonging to such species are unknown till present. Species of the genus *Asphondylia* occurring in the Palaearctic Region have not been revised since Rübsaamen (1916). Summarization of species described in the Palaearctic Region up to the present was given by Skuhravá (1986). At present, 51 species of the genus *Asphondylia* were described from the Palaearctic Region. Unfortunately, it was found that the original material of most species of the genus *Asphondylia* has been lost and is not available for taxonomical studies. One of the present authors (M. Skuhravá) gathered in her collection during her faunal investigations in Europe larvae, pupae and adults of the majority of species of the genus *Asphondylia*. She has in her collection also several undescribed species occurring in the territory of Europe.

Nevertheless, because of the narrow specific connection of the gall midge species with its host plant species which had developed in the process of the evolution of organisms in the ancient past of the world and is considered to be a result of the long-term processes of evolution of plant- animal relations, many gall midge species of the genus *Asphondylia* are host specific and may be determined at present if the host plant species and the shape of the gall developing on such host plant species are available.

The situation is even more complicated. Orphanides (1975) discovered during his study in Cyprus that *Asphondylia gennadii* (Marchal, 1904), larvae of which cause galls on pods of carob (*Ceratonia siliqua*), requires an alternate hosts during the summer. Harris (1975) evaluated morphologically these adults and came to the conclusion that it is impossible to distinguish adults of *Asphondylia gennadii* from adults reared by Orphanides from *Capsicum annuum*, *Capparis spinosa*, *Urginea maritima*, *Asphodelus fistulosus*, *Solanum tuberosum*, *Hypericum capsicum* and *Sinapis* spp. but it is possible to distinguish them from adults of *Asphondylia verbasci* (Vallot, 1827) according to the number of setae on the frontoclypeus. Later Gagné & Orphanides (1992) corroborated the results of Harris (1973) and concluded that pupae and larvae from the above mentioned



Figs 19–20. 19 – terminal stem gall of *Asphondylia anatolica* sp. n. on *Astragalus lagurus*; 20 – distribution area of *Astragalus lagurus* in Turkey according to data of Davis (1970) (white circles) and occurrence of galls of *Asphondylia anatolica* sp. n. at Tokat (black circle); occurrence of *Asphondylia* sp. at Mt. Hermon in Syria (black quadrate)

host plants are anatomically identical and that *Asphondylia gennadii* is a Palaearctic generalist species analogous to the Nearctic species *Asphondylia websteri* Felt, 1917 (Gagné & Woods 1988).

On the other hand, Yukawa & Ohsaki (1988) came to the conclusions in their studies about *Asphondylia baca* Monzen, 1937, larvae of which cause galls on *Ampelopsis brevipedunculata*, and *Asphondylia aucubae* Yukawa et Ohsaki, 1988, larvae of which cause galls on *Aucuba japonica*, that both species are morphologically quite similar but it is possible to distinguish them biologically.

We evaluated morphological characters of adults and pupae of *Asphondylia anatolica* sp. n. and came to the conclusion that it is not possible to distinguish adults from its related species, *Asphondylia sarothamni* Loew, 1850, larvae of which cause galls on buds and pods of *Sarothamnus scoparius* but it is possible to do it on the pupal stage.

Based on the shape of upper and lower frontal horns, *Asphondylia anatolica* sp. n. belongs in the *Asphondylia sarothamni*-group which is characterized by the presence of bifid upper and trifid lower frontal horns. Each species has these horns of specific shape. Dorsal part of the 7th and 8th abdominal segments is covered with spines which number, size and placement differ in both mentioned species.

The distribution area of *Asphondylia anatolica* sp. n. is restricted to small area in stony desert in northern Turkey where large complex galls occur on few host plants only and where probably only one generation develops a year. Also these biological and ecological characters indicate that *Asphondylia anatolica* is an independent species. It is also in the harmony with opinion of Gagné about *Asphondylia* species developing on *Atriplex* spp. in southern part of North America (see Hawkins et al.1986).

Acknowledgements

The authors would like to express their thanks to Dr K. M. Harris, Ripley, Woking, Surrey, UK, for his critical reading, advice and valuable comments on the manuscript.

REFERENCES

ANONYMOUS 1994 *Ortalama, Ekstrem Sıcaklık ve Yagıs Degerleri Bülteni* [*The Bulletin of Average, Extreme temerature and precipitation values (Daily – Monthly)*]. Ankara. T. C. Basbakanlık D M I. Genel Mudurlugu, 678 pp (In Turkish)

DAVIS P H 1970 *Flora of Turkey and the East Aegean Islands. Vol. 3.* Edinburgh: Edinburgh Univ Press, 628 pp

GAGNÉ R J & ORPHANIDES G. M 1992· The pupa and larva of Asphondylia gennadii (Diptera: Cecidomyiidae) and taxonomic implications *Bull. Entomol Res* **82** 313–316.

GAGNE R. J & WOODS W M 1988 Native American plant hosts of **Asphondylia** websteri (Diptera Cecidomyiidae) *Ann Entomol Soc Amer* **81** 447–448

HARRIS K M 1975: The taxonomic status of the carob gall midge, Asphondylia gennadii (Marchal), comb n (Diptera, Cecidomyiidae), and of other Asphondylia species recorded from Cyprus. *Bull Entomol Res* **65** 377–380

HAWKINS B A , GOEDEN R D. & GAGNÉ R. J. 1986: Ecology and taxonomy of the Asphondylia spp. (Diptera, Cecidomyiidae) forming galls on Atriplex spp. (Chenopodiaceae) in southern California *Entomography* **4** 55–107.

HOUARD C. 1908–1909: *Les zoocécidies des plantes d'Europe et du Bassin de la Méditerranée.* Paris: A Hermann et fils, 1365 pp

HOUARD C. 1922–1923· *Les zoocécidies des plantes d'Afrique, d'Asie et d'Océanie.* Paris: J. Hermann, 1056 pp

NOIRFALISE A. 1987: *Map of the natural vegetation of the member countries of the European Community and the Council of Europe.* Luxembourg. Environment and Natural Resources Division Council of Europe, 80 pp.

ORPHANIDES G M 1975 Biology of the carob midge complex, Asphondylia spp (Diptera, Cecidomyiidae) in Cyprus *Bull Entomol. Res* **65** 381–390.

Rubsaamen E H 1902 Mittheilung uber die von Herrn J Bornmuller gesammelten zoocecidien *Zool Jahrb Jena* **16** 243–336

Rubsaamen F H 1916 Cecidomyidenstudien V Revision der deutschen Asphondylarien *Sber Ges Naturf Freude Berl* **1916** 1–12

Skuhrava M 1986 Cecidomyiidae Pp 72–297 In Soós Á & Papp L (eds) *Catalogue of Palaearctic Diptera Vol 4 Sciaridae-Anisopodidae* Budapest Akademiai Kiado, 441 pp

Skuhrava M, Skuhravy V & Brewer J W 1984 Biology of Gall Midges Pp 169–222 In Ananthakrishnan T N (ed) *Biology of Gall Insects* New Delhi, Bombay, Calcutta Oxford & IBH Publishing Co, 362 pp

Tutin T G, Heywood V H, Burges N A, Valentine D H, Walters S M & Webb A A 1968 *Flora Europaea Vol 2 Rosaceae to Umbelliferae* Cambridge, Cambridge Univ Press, 420 pp

Udvardy M D F 1975 *A classification of the biogeographical provinces of the world* Switzerland, Morges IUCN Occasional Paper No 18 48 pp

Yukawa J 1985 Comparison between the soybean pod gall midge, Asphondylia sp and its exotic relative, Asphondylia ervi Rubsaamen *Mem Fac Agr Kagoshima Univ* **20** 183–187

Yukawa J & Ohsaki N 1988 Separation of the Aucuba fruit midge, Asphondylia aucubae sp nov, from the Ampelopsis fruit midge Asphondylia baca Monzen (Diptera, Cecidomyiidae) *Kontyû Tokyo* **56** 365–376

Acta Soc Zool Bohem. **62**: 226, 1998
ISSN 0862–5247

BOOK REVIEW

COX F E G, KREIER J. P. & WAKELIN D., volume editors: **Parasitology**, In COLLIER L., BALOWS A. & SUSSMAN M., general editors **Topley & Wilson's Microbiology and Microbial Infections. Volume 5** 9th edition. London, Sydney, Auckland, Arnold, a member of the Hodder Headline Group, 1998 Co-published in USA New York, Oxford University Press. XXXIV + 701 pages Format 195×270 mm Hard cover. Price of full set (6 volumes) Lstg 995 00 ISBN 0 340 663200 (Volume 5) – ISBN 0 340 614706 (Full set)

Topley & Wilson is used the world over as the definite reference for microbiologists and infectious disease specialists Since the first edition in 1929, this publication has seen various modifications in the form and content The inclusion of a volume devoted to parasitic infections is a new initiative As emphasized in the volume editors preface, the impact of parasitic diseases in developing countries is enormous, but they are no longer confined to such areas The rapid spread of quick and affordable international travel has meant that parasitic infections are frequently imported into temperate regions by immigrants and returning travelers Many infections once thought to be harmless are now known to be life-threatening in immunocompromised individuals Parasites have the capacity to develop resistance to drugs, the resistance to antimalarials being the most spectacular The control of vectors has been hampered by the development of insecticide resistance Parasitic diseases in some regions have been successfully eliminated, such as drancunculiasis and onchocerciasis in Africa On the other hand, new parasite species, such as microsporidians, emerged in immunocompromised individuals The overall objective of this volume is to enhance, update and strengthen the literature familiar to professionals working in the field of tropical and parasitic diseases The book is composed of three parts **Part I: General Considerations** incorporates 5 chapters providing insights into general terms The history of medical parasitology is outlined by professor Cox – the editor of **The Wellcome Trust Illustrated History of Tropical Medicine** which appeared in print in 1996 Following chapters embrace world-wide importance of parasites and epidemiology of parasitic infections Immunology and immunopathology of human parasitic infections are compiled here with special reference to novel concepts including latest advances in immunological terms Pointed out are the cytokine network and characteristic features of immunity to protozoa and helminths Furthermore, there is a chapter discussing concepts of control and eradication, stratification of parasitic diseases in relation to epidemiology and approaches to control Included are tabular overviews of public health importance of parasitic infections, stratification of malaria and other major parasitic diseases, recent epidemics, diagnostic tools recommended by WHO, and more **Part II: Protozoa** embrasses chapters 6 through 23 Introductory general chapter is concerned with cellular organization and classification of parasitic protozoans as eukaryotic organisms Featured are the general morphology of protozoan cell Chapter on classification of parasitic protozoa is presented when discussing general characters of principal protozoan taxa There is a traditional classification scheme including four phyla **Sarcomastigophora, Apicomplexa, Microspora and Ciliophora** Another scheme presents the utilitarian and user-friendly hierarchical classification offered by Corliss (1994) restricted here on protozoan parasites of medical interest This scheme includes five phyla and has been completed up to the order level Three new orders appeared here **Vestibuligerida, Acanthopodida and Euamoebida** An appendix contains a check list of the protozoic parasite species in humans In following special chapters significant attention is paid to particular protozoan infections Titles of these chapters are introduced partly by names of parasites, partly by names of diseases Each chapter is constructed by a general frame Discussed are classification, structure and life cycles, biochemistry, molecular biology and genetics, clinical aspects, immunology, pathology, diagnosis, epidemiology (including reservoir hosts) and control, chemotherapy and vaccination All the authors are internationally accredited authorities in the field, some of them contributed to the multi-volume edition on "Parasitic Protozoa" under editorship of P Kreier and J R Baker Looked at are intestinal amoebae, opportunistic amoebae, giardiasis, trichomonads and intestinal flagellates, leishmaniasis in the Old World and neotropical *Leishmania* species, African trypanosomes, toxoplasmosis, *Sarcocystis*, *Isospora* and *Cyclospora*, cryptosporidiosis, babesiosis in humans, malaria, microsporidians, pneumocystosis and *Balantidium coli* **Part III: Helminths** is devoted to helminthic infections in chapters 24 through 35 Introductory chapter comprises the nature and classification of flatworms, roundworms and thorny-headed worms Taxonomical schemes of parasitic helminths are well-arranged and complete (authorships/data) An account of helminth groups which occur as parasites in humans is presented in a form of a summary of morphological features, pathogenicity and modes of infection Following chapters are concerned with assemblages of helminths of medical importance arranged according to the taxonomical, biological or pathological aspects Titles of particular chapters are introduced by taxonomical or nosological names In the chapter on schistosomes or blood flukes three species, *Schistosoma japonicum*, *S mansoni* and *S haematobium* and also other species which product infections in humans are examined There is a list of intermediate snail hosts including their geographical distribution Furthermore, immune responses and vaccination comprising the vaccine candidates with data on antigen identity and size (kDa) are looked at in detail A concise chapter on lung and liver flukes follows Among intestinal tapeworms outlined are cyclophyllidean and pseudophyllidean cestodes comprising a detailed treatise of cysticercosis Among gastrointestinal nematodes described are ascarids, hookworms, trichurids and pinworms Following chapters ensure covering of *Strongyloides* and *Capillaria* *Trichinella* and *Toxocara*, lymphatic filariasis, onchocerciasis, *Angiostrongylus* and less common nematodes, and dracunculiasis Each chapter contains a list of references discussing particular taxa of parasitic protozoans and helminths Thus, presented is a comprehensive synopsis of parasitological bibliography The volume is amply illustrated by a wealth of figures composed of schematic line drawings featuring life cycles and forms of parasitic protozoans and metazoans, cell structures, geographic maps, diagrams and histograms, immunological, pathological and epidemiological phenomena, sequences of clinical signs, flow charts and metabolic pathways Micro- and macrophotographs, partly in colour, present details of surface and internal ultrastructures, histological sections and blood films, isoenzyme profiles, clinical aspects, organ, skin and eye changes, x-rays, tomo- and ultrasonoscans, arthropod vectors and conchae of snail intermediary hosts Numerous tabular overviews present taxonomical classification schemes, prevalence data, epidemiological characteristics, diagnostic and therapeutic shedules, and preventive measures Written by the world s foremost authorities in the field, this remarkable guide-book presents one of the best single-volume texts dealing with medical parasitology Parasitologists might only regret that a special part discussing parasitic arthropods – ectoparasites and vectors – is not included here In the heading of the book listed are titles and contents of volume 1 **Virology**, volume 2 **Systematic Bacteriology**, Volume 3 **Bacterial Infections**, volume 4 **Mycology and** volume 6 **Cumulative Index** The set of 6 volumes includes 4,500 pages, 1,250 black & white illustrations, 250 colour illustration, 633 tables, 400,000 references and is over 65% bigger than the previous edition There is a team of 340 expert contributors – more than double the last edition The 9th edition is available also on CD-ROM

Jindřich Jíra

Acta Soc. Zool. Bohem. **62**: 227–253, 1998
ISSN 0862–5247

Reproductive biology of the Central European *Aphodius* species with large scutellum (Coleoptera: Scarabaeidae: Aphodiinae)

Jan VITNER

Library of the Czech Entomological Society, Viničná 7, CZ–128 00 Praha 2, Czech Republic

Received June 18, 1998; accepted September 24, 1998
Published October 30, 1998

Abstract. Oviposition habits, larval behavior, and ontogeny of the following dung beetle species were studied under laboratory conditions: *Aphodius* (*Coprimorphus*) *scrutator* (Herbst, 1789), *A.* (*Teuchestes*) *fossor* (Linnaeus, 1758), *A.* (*Colobopterus*) *erraticus* (Linnaeus, 1758), *A.* (*Eupleurus*) *subterraneus* (Linnaeus, 1758), and *A.* (*Otophorus*) *haemorrhoidalis* (Linnaeus, 1758). Additional field observations on the oviposition habits are given for *A. fossor* and *A. erraticus*.

The oviposition habits of *A. scrutator* and *A. fossor* were found to vary from egg chambers positioned directly in the dung pad to spherical brood masses separated from the dung pad by a soil layer. L_1, and to some degree L_2 live in brood masses where they are formed, eating them from inside. The oviposition habits are less variable in *A. erraticus*, where brood mass and egg chamber in soil at the lower end of the brood mass are formed as a rule. The larvae feed on the brood mass during all three instars, eating it from outside. *A subterraneus* and *A. haemorrhoidalis* do not construct nests. It was found that females of *A. scrutator* and *A. fossor* are able to lay at least 50 eggs each. Fragmentary data are presented indicating that adult individuals of *A. scrutator* are aggressive in the course of the competition for space suitable for oviposition. This may be a certain form of subsocial behavior. The voltinity and seasonal dynamics of reproduction of the studied species are discussed.

Oviposition habits, larval behavior, structure of pupal chambers, and morphological adaptations of the larvae of *A. erraticus* and *A.* (*Colobopterus*) *quadratus* Reiche, 1842 are related to each other, and their systematic importance is discussed. The results indicate that at least some of the species included in the subgenus *Colobopterus* Mulsant, 1842 form a natural group. A modified schema of the evolution of the oviposition habits in the genus *Aphodius* Illiger, 1798 is presented. An opinion is expressed, that speaking of evolutionary trends is better than to typologically classify the oviposition habits into discrete units, while studying the evolution of the oviposition habits in this genus.

Reproduction, nest-like oviposition habits, fecundity, ontogeny, larval behavior, larval morphology, evolution of nesting behavior, systematics, Coleoptera, Scarabaeidae, Aphodiinae, *Aphodius*

INTRODUCTION

The first report on the brooding habits of beetles of the genus *Aphodius* Illiger, 1798 was published by Xambeu (1901: 56). He reported on *A. scrutator* (Herbst, 1789). Xambeu's data are probably based not only on his own observations because some of the data are evidently incorrect (e.g. repeated relocation of the pieces of dung, construction of the brood balls from relocated pieces of dung, information that larvae stay in brood balls during their entire ontogeny, incl. pupation). It is probable, that Xambeu found brood masses with eggs, and added speculations, influenced by previous studies by J. H. Fabre. According to this speculation, nesting behavior of *A. scrutator* is similar to the same behavior of burrowers from the subfamily Coprinae (cf. Fabre 1897, 1899). Morphological differences between the representatives of the Aphodiinae and Coprinae (particularly less developed hind tibiae and clypeus in *Aphodius*, and different body shape) indicated that

Xambeu's data cannot be accepted Because of this, Xambeu's paper was disregarded during the next half of the century, and the presence of the nesting behavior in *Aphodius* species was considered highly improbable (see Lengerken 1954. 284)

Nevertheless, studies performed in the 1980s and 1990s on *Aphodius* species inhabiting Europe (Rojewski 1983, Zunino & Barbero 1990, Palestrini & Barbero 1994, Zunino et al 1994, Barbero & Palestrini 1995), and Japan (Hosogi 1985, Yoshida & Katakura 1992) confirmed, that certain nesting behavior is part of their reproductive behavior Yoshida & Katakura (1992) discussed the evolution of oviposition habits in *Aphodius* and presented their classification

In the present paper, observations on the reproductive biology of five Central European *Aphodius* species with large scutellum (cf Dellacasa 1986) are presented All European species, for which nesting behavior was documented, belong in this group of *Aphodius* dung beetles Some of the observations were obtained on beetles reared during a study of the morphology of their larvae (cf Vitner 1996), while some beetles were specially reared for the study of their oviposition habits Laboratory observations were supplemented with a limited amount of the field data

My observations on the oviposition and nesting behavior of *Aphodius* dung beetles were compared with one another and with published data Intraspecific variability of oviposition habits and feeding behavior of the larvae were studied Reproductive strategies of *Aphodius* species with nesting behavior are discussed, and characterized In addition, Yoshida & Katakura's (1992) model of the evolution of oviposition habits is discussed

METHODS

Adult beetles were kept in glass jars, plastic boxes, and wooden frames (see Table 1) The volume of glass jars was 0 5, 0 7, 1, and 4 litres, respectively, while their diameter was 6, 6 5, 10, and 13 5 cm respectively The plastic boxes were quadratic, and measured 16×9 5×9 5 cm Wooden frames were covered with glass panes from both sides (see Prasse 1957) Their dimensions were 34×22×1 3 cm and 24×22×1 cm, respectively Front part of plastic boxes was cut out, excepting a 2 cm broad belt and after each control again pasted on back with Herkules dispersion gum (Druchema, Praha)

Brooding containers were filled with soil, the layer of which reached ca 10–15 cm in glass jars, ca 10 cm in plastic boxes and 4–6 cm below the upper end of panes in wooden frames, respectively Jars and boxes were covered with fine netting, held by a rubber band Soil was collected on gardens under sods and mixed with ca 10–20 per cent sand The soil was sieved before use, and all macroscopic animals were removed Beetles were fed once with fresh sheep or cattle dung (collected immediately after defecation to ensure that no other insects were present in it) Most of the soil surface in the containers was covered with a 2 5–3 cm thick layer of dung, leaving 1–2 cm broad side belt uncovered

Brooding containers were situated outdoors (under shelter), in heated and in unheated rooms They were not sheltered Wooden frames were positioned with one glass pane facing wall and the other facing a window

Controls were done in the following manner In jars, dung and at least half of the soil were removed In plastic boxes, front part was removed, and an outer, 2–3 cm thick layer of dung and soil was scratched out by a pincette After every control, the removed soil was returned back, and the observed situation was noted and figured Beetles in wooden frames were controlled through the glass, and the situation was traced by ink on a sheet of cellophane Sometimes these broods were controlled directly, after removal of a glass pane After such a control, the pane was returned carefully, so to cause as little damage to the brood as possible

For particular data on individual broods see Table 1 Broods founded for the study of the oviposition habits are marked with an asterisk (*) Controls, during which photographs and figures used in this paper were obtained, are also marked Numbers of observed or collected individuals are not given because only part of the dung pad and the soil was controlled in most instances All controls are listed The controls were cancelled, when living or fresh dead individuals of the filial generation were found Unsuccessful broods are not listed in the table

Field observations on the brood masses of *A fossor* and *A erraticus* are included For details see Results All data were obtained during my faunistic reseach in 1985–1994 in Bohemia, Moravia, and Slovakia

Nomeclature of dung beetles with large scutellum follows Dellacasa (1986), nomeclature of other Central European species was adopted from Kral (1993), while that of non-European species follows Dellacasa (1988)

MATERIAL

Adult dung beetles used in this study were collected in Bohemia and Slovakia The numbers in parentheses after the name of each locality refer to codes of faunistic grid mapping fields (see Zelený 1972) J Vitner lgt et det. in all cases, if not otherwise indicated

A scrutator Slovakia or Plešivecká planina (73–7488), Bohemia bor Poplze (5550)

A fossor Slovakia or : Somotor (7696), Zádiel (7391), Silica (7489) ; Bohemia bor : Odolice (5548), Poplze (5550), Bohemia centr : Lysá nad Labem-Karlov (5755).

A erraticus Bohemia centr Praha-Hostivař (5953), Lysá nad Labem-Karlov (5755), Slovakia centr : Horné Pribelce (7881), D Král lgt et det

A subterraneus Slovakia or . Somotor (7696), Bohemia centr . Lysá nad Labem, race-course (5755), Lysá nad Labem-Karlov (5755), Slovakia or Zemplín/Cejkov (7596).

A haemorrhoidalis Slovakia or. Hrhov (7390), Silica (7489), Somotor (7696); Bohemia bor. Raná (5548); Bohemia centr : Lysá nad Labem-Karlov (5755)

Specimens of adults and pre-imaginal stages are preserved in Pampel's solution, and deposited in the author's collection

RESULTS

Detailed data on the broods are given in Table 1. Numbering of individual broods corresponds with that in the text.

Mating behavior was not observed, and the same applies to nest building (with the exception of an observation of *A. erraticus*).

No differences were found between observations obtained in wooden frames on the side facing light source and on the reversed side. Hence, the data were combined.

Time schedule of the duration of individual stages and larval instars was reconstructed with respect to the "standard Central European field conditions", i.e. to such seasonal changes of temperature and rainfall, that are not much different from local long-term means at elevations below ca. 500 m a.s.l. in this century.

Aphodius (*Coprimorphus*) *scrutator* (Herbst, 1789)

Eggs were laid in egg chambers, whose structure and size approximately agreed with the observations by Barbero & Palestrini (1995). Almost all egg chambers were found in depressions in the bottom of dung pads (see Figs. 1–3), mostly well visible from outside. Some egg chambers were found in bottle-shaped structures (see Figs. 2 and 4), and in roughly spherical masses, separated from the dung pad by a 2–6 cm thick soil layer. Only one egg chamber was found directly in the dung pad, without showing any sign of a depression (see Fig. 14a). Oviposition sites widely ranged in shape, as shown in Figs. 14a–f, and 14i–k. Marked depressions prevailed in broods Nr. 3–5, but the prevalence was not significant. Maximum depth of a depression was ca. 27 mm. Some depressions were positioned close to each other, being even fused in three cases (see Figs. 5–6, and 14f). Two egg chambers in a single depression (as in Fig. 14g) were not recorded in this species. In the brood Nr. 2, where the soil was not rammed down as in broods Nr. 3–5, all egg chambers were found in spherical brood masses, separated from the dung pad by a soil layer (see Fig. 14k).

The eggs were glued with one end to the wall of the egg chamber, probably by droppings of the female (cf. Barbero & Palestrini 1995). When eggs remained intact in opened egg chambers, it was found, that they were approximately in a vertical position. Activities of females during "nest" formation and oviposition were not observed.

Oviposition sites were not observed in the field.

Nr	Locality	Date	Start	End	Place	Ad.	Box	Day	Obs	Day	Obs	Day	Obs	Day	Obs.	Day	Obs.	Day	Obs.	Day	Obs	Day	Obs
	Basic data on the broods							Results of controls															
								1		2		3		4		5		6		7		8	
	A. scrutator																						
1	Plešivecká planina	18 vii 1985	22 vii	19 ix	NH	3	1G	28	L2														
2	Poplze	15 vii 1987	17 vii	26 x	OB	2/5	4G	14	BM o L1	16	BM o L1	32	L2 L3	70	L3								
3* a	Poplze	4 vii 1988	5 vii	8 xi	NH	1/1	IF	13	OBS-BM	28	OBS-L3	47	OBS-L3	59	OBS-L3	74	OBS-L3	95	OBS-L3				
b	Poplze	4 vii 1988	5 vii	8 xi	NH	1/1	IF	13	OBS-BM	28	OBS-L3	47	OBS-L3	59	OBS-L3	74	OBS-L3	95	OBS-L3				
c	Poplze	4 vii 1988	5 vii	3 x	NH	1/1	sF	13	BM o L1	28	OBS-L3	47	OBS-L3	59	L3								
d	Poplze	4 vii 1988	5 vii	18 x	NH	1/1	sF	[3]13	OBS-BM	28	OBS L3	47	OBS-L3	59	OBS-L3	74	L3						
e	Poplze	4 vii 1988	5 vii	8 xi	OB	3/5	5G	47	L3	59	L3	74	L3	95	L3								
4*	Poplze	22 vii 1989	23 vii	15 vi	NH	0/1	PBx	13	o	[3]15	o L1	22	o L1	40	L2 L3	72	L3 (3 x)	205	L3 (6 ii)	248	P (18 iv)	294	fcA
5* a	Poplze	4 vii 1990	5 vii	22 xi	OB-NH[1]	1/2	PBx	[4]18	BM L1 L2	22	BM L1 L2	24	L1 L2	77	L3								
b	Poplze	4 vii 1990	8 vii	23 vii	OB-NH[1]	2/2	PBx	6	BM o	[5]10	BM o	15	BM L1	17	BM L1								
c	Poplze	4 vii 1990	6 vii	9 i	OB-NH[1]	10	4G	44	L3	77	L3	108	L3	156	L3								
d	Poplze	4 vii 1990	6 vii	9 i	OB-NH	10	4G	[6]31	L2, L3	74	L3	156	L3										
	A. fossor																						
1	Somotor	25 vi 1986	5 vii	24 vii	NH	13	3G	15	L2 L3	28	L3	52	fcA										
2	Zádiel	4 v 1987	15 v	12 vii	NH-OB[2]	5	0.7G	33	o L1 L2	82	L3	89	L3 P fcA										
3*	Poplze	4 vii 1988	5 vii	3 x	NH	1/1	IF	13	OBS-L3	47	OBS-P	59	fcA										
4	Silica & Somotor	18 & 21 vi 1990	27 vi	22 xi	NH	2/2	1G	21	L3	148	fcA												
5*	Poplze	4 vii 1990	6 vii	7 iii	NH-H[3]	8	PBx	6	BM o L1	[7]10	L1 L2	18	L2 L3	46	P	106	fnA fcA	182	fnA fcA				
6	Lysá n.L. - Karlov	5 vii 1992	7 vii	9 ix	NH	2/2	PBx	16	L2 L3	35	P	46	fcA[4]	55	fcA	61	fcA						
7*	Lysá n.L. - Karlov	2 vii 1992	5 vii	14 vii	NH	0/2	IF	2	BM o	8	BM o L1												
8*	Odolice	30 vi 1994	6 vii	14 vii	NH	1/1	IF	1	OBS-BM	[10]4	OBS-BM	9	L2 L3										
9* a	Odolice	20 vii 1994	22 vii	29 vii	NH	1/1	sF	2	OBS-0	5	OBS-0	7	L1 L2[5]										
b	Odolice	20 vii 1994	22 vii	10 viii	NH	1/2	PBx	3	BM o	5	BM L1	7	BM L1	12	L2 L3	19	L3						
c	Odolice	20 vii 1994	22 vii	2 ix	NH	1/2	PBx	3	BM, o	5	BM, o, L1	7	BM, L1, L2	9	BM, L1, L2	16	L3	27	wL3	35	P	41	fcA
	A. erraticus																						
1	Praha - Hostivař	18 v 1989	19 v	1 viii	OB	7	4G	14	0[6]	42	P	62	P										
2 a	Praha - Hostivař	9 vii 1991	11 vii	18 ix	NH	8	4G	12	L3[4]	21	wL3 P	60	fcA										
b	Praha Hostivař	9 vii 1991	11 vii	18 ix	NH	8	4G	12	L3[4]	21	P	60	fcA										
3	Praha Hostivař	30 vii 1991	31 vii	18 ix	NH	11	4G	12	L2 L3[7] wL3	49	fcA												
4	Lysá n.L. Karlov	24 v 1992	25 v	23 vi	NH	3/3	PBx	16	L3[7]	29	fcA[8]												
5	Lysá n.L. Karlov	14 vi 1992	14 vi	25 vi	NH	8	PBx	4	0	8	0	11	L2										
6* a	Lysá n.L. - Karlov	5 vii 1992	6 vii	14 vii	NH	4	PBx	8	BM L2 L3														
b	Lysá n.L. - Karlov	5 vii 1992	6 vii	31 vii	NH	5	PBx	8	0	25	P												
7* a	Lysá n.L. - Karlov	22 vi 1992	23 vi	31 vii	NH	2/2	sF	1	OBS-BM	2	OBS-BM o	3	OBS-BM L1 L2	5	L1 L2 L3	8	OBS-BM L3						
b	Lysá n.L. - Karlov	22 vi 1992	23 vi	17 vii	NH	3/3	sF	1	OBS-BM o	2	OBS-BM o	3	OBS-BM	18	OBS-BM P	19	OBS-BM, P	20	OBS-BM, P	22	OBS-BM P	25	fnA
c	Lysá n.L. - Karlov	22 vi 1992	23 vi	28 vi	NH	3/4	sF	1	OBS-BM	2	OBS BM o	3	OBS-BM	[7]5	o L1 L2								
8*	Horní Přibelce	27 v 1995	30 v	11 vi	NH	7	PBx	2	0	12	BM, L3												
	A. subterraneus																						
1	Somotor	25 vi 1986	5 vii	2 viii	NH	8	PBx	16	0	28	L3 wL3												
2	Lysá n.L. race-course	28 iv 1987	28 iv	17 vi	NH-OB[9]	11	4G	49	L2	80	L3												
3	Zemplín/Čejkov	22 vi 1990	27 vi	21 ix	NH	10	4G	18	L1 L2 L3	57	fcA	88	fcA										
4	Lysá n.L. - Karlov	24 v 1992	25 v	31 vii	NH	7	4G	21	L1 L2 L3	29	L1 L2 L3	38	L1 L2 L3 wL3 P	52	wL3 P fnA	67	P fnA, fcA						
5	Lysá n.L. Karlov	14 vi 1992	15 vi	11 viii	NH	8	PBx	22	L2 L3	46	L3	57	fcA										
6*	Lysá n.L. Karlov	21 vi 1993	28 vi	[1]10 viii	NH	2/3	sF	13	L1, L2, L3														
	A. haemorrhoidalis																						
1	Hrhov & Somotor	24 & 25 vi 1986	5 vii	2 viii	NH	20	PBx	16	L1 L2 L3	28	L3 P												
2	Raná	24 v 1988	30 v	2 ix	OB	4	0.5G	25	L1	91	fcA												
3	Raná	7 vii 1989	10 vii	29 viii	OB	12	4G	11	L1 L2	23	L2 L3 wL3	50	fcA										
4	Silica	18 vi 1990	27 vi	21 ix	NH	12	4G	19	L1 L2 L3	57	fnA, fcA	86	fcA										
5*	Lysá n.L. - Karlov	2 vii 1992	3 vii	17 vii	NH	7	sF[11]	[10]4	o, L1	8[11]	L1, L2	14	L3										

[1] Moved on 21 vii (15 days after the foundation of the brood)

[2] Moved on 22 v (7 days after the foundation of the brood)

[3] Moved on 3 xii (119 days after the foundation of the brood)

[4] These adults were unsuccessfully used on 31 vii (52 days after the foundation of the brood) to found new broods in IF, sF and PBx

[5] In chambers in the dung pad without BM

[6] Only the dung pad was controlled

[7] With remains of BM

[8] It was impossible to decide whether the individuals belonged to the parental or the filial generation

[9] Moved on 22 v (24 days after the foundation of the brood)

[10] Four broods (all in wooden frames) were founded on 24 vii but dung pads became mouldy. The broods were renewed, but only this one was successful

[11] This brood was moved in PBx on the 8th day after its foundation (11 vii)

* Fig 15 prepared

* Figs 2-4 prepared

* Figs 5-7 prepared

* Fig 1 prepared

* Figs 8-9 prepared

* Figs 10-11 prepared

* Fig 16 prepared

* Figs 12-13 prepared

* Fig 17 prepared

The broods Nr. 3a–d, and Nr. 4 contained only one female each. When the broods Nr. 3a–b were cancelled on 9 January 1989 (after 157 days of existence), only disintegrated remains of dead larvae were found, and their exact numbers could not be estimated. When the broods Nr. 3c (4th control), and 3d (5th control) were cancelled, 37 and 43 L_3, respectively, were found. In the brood Nr. 4, the entire contents of the container were checked, and 51 eggs and larvae were found. It means, that a single female of *A. scrutator* is able to produce at least 50 eggs.

First L_1 were found after 13 days, L_2 after 18 days, and L_3 after 28 days respectively. Exact data were not obtained, but it can be estimated, that L_1 hatch earlier than 10 days after the oviposition, and that L_1 and L_2 last ca. one week to 10 days each. Adults of the filial generation were reared only once, but it is highly probable (cf. data in Table 1), that all L_3 hibernate (irrespective of the timing of the oviposition), and that they pupate in the soil in spring. The pupa develops for ca. 1 month. Hence, I consider *A. scrutator* to be a strictly univoltine species with hibernating L_3. The reproductive season is summer, and perhaps also the end of spring. [In addition to the broods listed in Table 1, I unsuccessfully kept adults found on 18 June 1990 at Silica. The brood was founded on 27 June.] In the field, I found adults from the middle June to the middle October.

L_1 (with the exception of newly hatched ones) were found in egg chambers, widened and deepened by the feeding activity of the larvae. In a few cases, only a skin remained from the brood mass. Some egg chambers were already connected by a tunnel with the cavity, formed by the female during the creation of brood mass by stuffing the dung. L_1 were mostly found in the egg chamber, sometimes in the tunnel. When disturbed, some larvae tried to escape through the tunnel into the cavity. Most of L_2 were found in the same position, but the tunnel was almost consistently present. It was absent in two cases only. In the first case, the egg chamber in the brood mass was connected with the dung pad (Fig. 7). In the other case, brood mass was separated from the dung pad by a soil layer. In two cases (broods Nr. 4 – 4th control, and Nr. 5d – 1st control, respectively), L_2 were found together with ca. 50 L_3 in a totally decayed dung pad, incl. its upper part. Exuviae of L_2 were found in several chambers of L_3 during the 4th control of the brood Nr. 4.

L_3 were mostly found in chambers in the dung pad, while some were found in chambers in the soil under the dung pad, in a maximum depth of 30 mm. In such cases, the tunnel connecting the chamber with the decayed dung pad was well visible (brood Nr. 5d – 1st control; see Figs. 8–9). Some of the larvae in the outdoor brood Nr. 3e were found creeping on the top of the dung pad during the 4th control. Probably, they tried to find a way to better burrowing conditions, because the brood container was already in process of freezing in that night.

The pupae were found in pupal chambers placed in the soil. The walls of the chambers were already stiffened and rather dry in all cases. Hence, it was impossible to find out, whether they were lined by L_3 with a thin layer of their droppings, or not.

Behavior of adult females of *A. scrutator*, and behavior of hatched larvae in the course of their ontogeny can be summarized as follows: The female excavates under a dung pad a depression.

<<

Table 1 Data on the broods of the studied *Aphodius* species

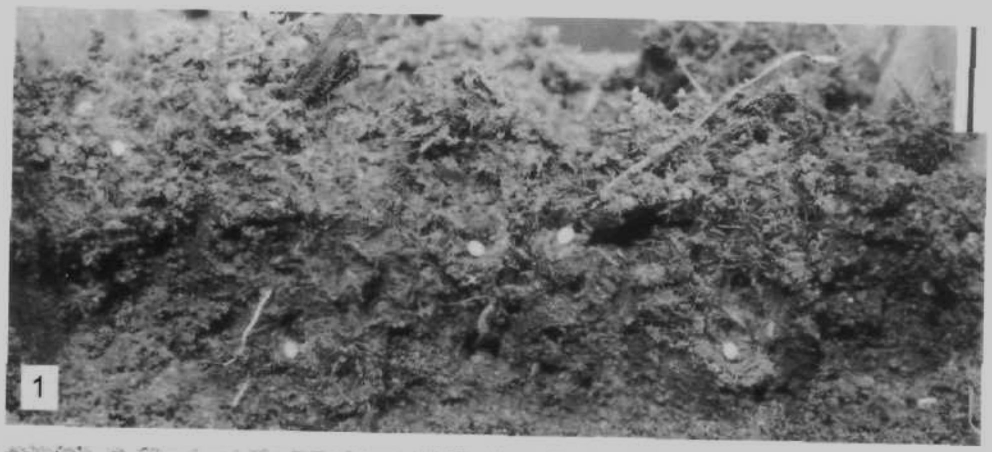
* – broods founded for the study of oviposition habits; date – date on which adults were collected, start date on which the brood was founded; end – date of the last control; place – position of the brood, OB – outdoor broods, NH – not heated rooms; H – heated rooms, Ad – number of unsexed adults, or males/females, box – brooding container; G – glass jar (the number means volume in litres), lF, sF – larger, and smaller wooden frames covered with glass panes, PBx – plastic boxes; day – control day (from the foundation of the brood), obs. – what was observed, OBS – observed only through glass pane, 0 – negative observation (except of adults of the parental generation), BM – brood mass, o – egg, L1, L2, L3 – larvae of the 1st, 2nd, and 3rd instar, respectively, wL3 – white larvae of the 3rd instar prepared for pupation, P – pupae, tnA – teneral adults from the filial generation, fcA – fully colored adults from the filial generation. Instars printed in bold were prevailing. For the size of brooding containers see Methods

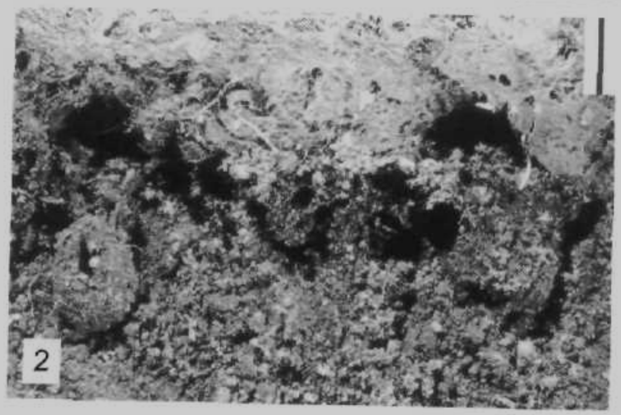
Then she forms from the dung an egg chamber in the cavity, lays and glues on an egg, and closes the chamber. Then she fills the remaining part of the cavity with dung. Sometimes, an egg chamber is placed inside the lower layer of the dung pad. In some other cases, egg chamber has no direct connection with the dung pad, and is included in a brood mass, isolated from the dung pad by a soil layer. L_{1-2} use up the food in the brood mass, and then form (by eating or digging) a tunnel to the dung pad. There, L_2 continue to feed on the dung in newly formed chambers. L_3 feed in all layers of the dung pad. In the fall, L_3 go down to deeper soil layers to hibernate. They pupate when temperature increases (probably in the first half of the spring). Further increase of temperature in the late spring probably triggers the activity of newly hatched adults.

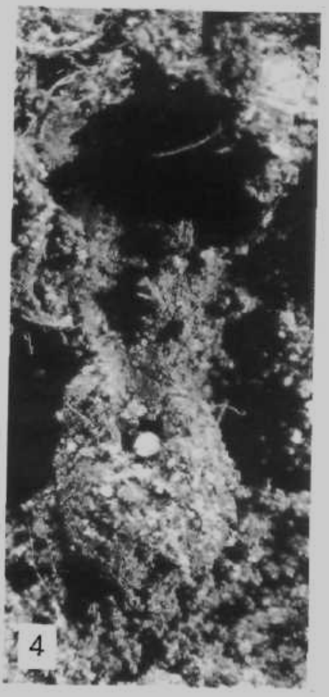
Note. Field experiments by Chromý (1979) indicate, that *A. scrutator* strongly prefers cattle dung pads. [It is the only Central European species, found by myself exclusively in cattle dung pads.] Central European *Aphodius* species reproduce in the warmest season, i.e from the late spring till the late summer/early fall. Of them, only *A. scrutator* almost surely seems to be univoltine. The larval stage is rather long (cf. data on other species), and large cattle dung pads provide the larvae with a sufficient amount of food. In this respect, two other observations deserve mentioning: (1) A female selected for the brood Nr. 4 was transported in a glass jar (volume = 250 mm^3), covered with a riddled cap, and filled to two thirds with soil and pieces of dung. In the jar, it was accompanied with 8–10 individuals of *A.* (*Acrossus*) *rufipes* (Linnaeus, 1758). Some 20 hours later, all of *A. rufipes* were found killed, with crushed and teared off heads and thoraces. It was confirmed, that no other animals were in the jar, except for the above mentioned individuals of *A. scrutator* and *A. rufipes*. (2) While collecting adults for the brood Nr. 5, I found in each of two cattle dung pads ca. 20 individuals of *A. scrutator*, but almost no other dung beetles. On the same day, and in the same locality, separate individuals of *A. scrutator* were regularly found also in cattle dung pads, positioned on drier, sunny places, together with individuals of *A. fossor*, which is roughly of the same size. (*A. rufipes* was found in that locality only in more moist, often partially shaded places.) Nevertheless, no individuals of *A. fossor* were found in the two, above mentioned dung pads. These observations indicate, that something like aggressive behavior, and even subsociality may exist in *A. scrutator*, e.g. the individuals compete for dung pads suitable for oviposition. The indication is vague and uncertain, but the observations should not be forgotten.

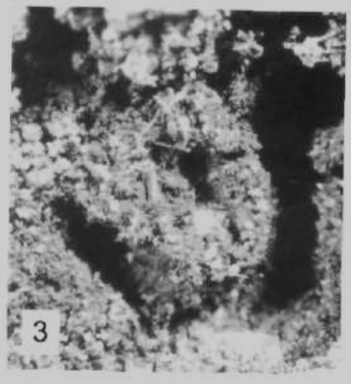
***Aphodius* (*Teuchestes*) *fossor* (Linnaeus, 1758)**

Oviposition habits are rather variable in this species (cf. Figs. 14a–i, and 14k). Some of the egg chambers in the broods Nr. 2, 5, 9b, and 9c, and all egg chambers in the broods Nr. 9a were found directly in the lower part of dung pads (Fig. 14a). The position of egg chambers was probably the same also in the brood Nr. 3, because no changes of the border between soil and dung pad were observed until L_3 appeared. Most of the egg chambers were found in shallow depressions, having a maximum depth of 14 mm (Fig. 14b–d). Egg chambers were positioned in deep bottle-shaped burrows in the brood Nr. 7, and probably also in the brood Nr. 8, where the depressions were deep, but their shape was not clearly visible through the glass pane (cf. Fig. 14i, and 16, respectively). Some egg chambers in the brood Nr. 5 were placed in spherical brood masses, separated from the dung pad by a soil layer. In each of the broods Nr. 9b and 9c, a broad depression was found (depth = = 7 and 12 mm, respectively), containing two egg chambers (Fig. 14g). In the brood Nr. 5, L_1 (during the 2nd control), and L_2 (during the 2nd and 3rd controls) were found just under the dung pad (Fig. 10). This may indicate that egg chambers were positioned in the soil under the dung pad (see below).

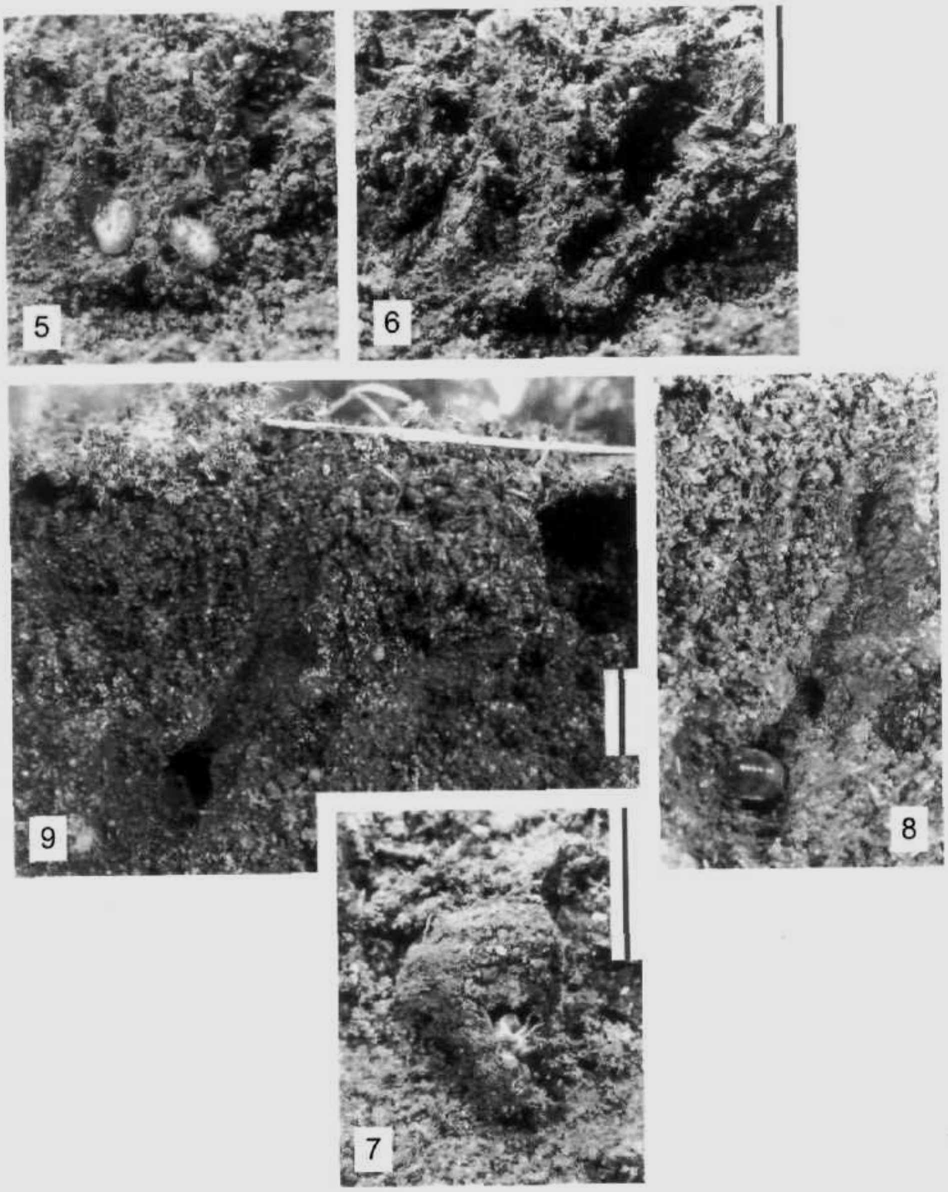

1


2


4


3

Figs 1–4. *Aphodius scrutator* (Herbst). 1 – Dung pad with brood masses; 2 – Lower part of the dung pad with two brood masses; 3–4 – Details of the brood masses from Fig. 2. Scale bar = 10 mm.



Figs 5–9. *Aphodius scrutator* (Herbst). 5 – Two L_2 in brood masses with tunnels leading to cavity; 6 – same situation without the larvae; 7 – L_2 in a brood mass without tunnel; 8 – L_3 in a secondary chamber in the upper layer of the soil with a tunnel leading to the dung pad; 9 – same situation without the larva. Scale bar = 10 mm.

Relevant behavior of females was not observed. Brooding activity did not last longer than 4 days in the brood Nr. 8, because shape of the brood mass did not change in days comming after the 4th day from the foundation of the brood (see Fig. 16).

The eggs were glued to the wall of each egg chamber. Position of the eggs varied: they were in a roughly vertical to almost horizontal position in the brood Nr. 7, while the position was almost horizonal in the broods Nr. 9b, and 9c, where the angle contained between the egg axis and the horizonal axis was always less than 20° (both plus and minus). The position of eggs in egg chambers found in the field was probably variable as well (see below).

In the field, the position of eggs was probably observed on 20 July 1994 at Odolice. On the bottom of a cattle dung pad, probaly less that one week old (the dung pad was covered with a thick crust, being compact and smooth inside), four depressions with egg chambers containing eggs were found. The depressions were up to 10 mm deep. Free ends of the eggs were elevated, but their exact position could not be estimated with any certainty, because the observation was done only after pieces of dung were separated from the dung pad, and the depressions were opened. In addition, this dung pad was laying on a track. An attempt to collect larvae from the eggs was not successfull, so that their identification could not be confirmed. At this locality, five cattle dung pads were controlled, all being approximately of the same age. The following *Aphodius* species were found: ca. 20 adults of *A.* (*Aphodius*) *fimetarius* (Linnaeus, 1758), ca. 10 *A. fossor*, 1 *A.* (*Bodilus*) *rufus* (Moll, 1782), and 1 *A. subterraneus*. [I found L_1 only inside of dung pads in the captive broods of *A. fimetarius* and *A. rufus*, but never in nesting depressions.]

The broods Nr. 3, 8, and 9a contained one female each. Six larvae were found in the brood Nr. 9a, and the female was dead and decaying already on the 7th day after the foundation of the brood. The brood Nr. 3 was checked only after adults of the filial generation. The following animals were found: 7 adults, 1 dead pupa, and 2 dead L_3. Overall, 7 L_2 and 44 L_1 were found in the brood Nr. 8. Hence, a single female is capable of producing a minimum of 50 eggs.

First L_1 were found 5 days after the foundation of the brood, first L_2 after 7 days, and L_3 after 9 days, respectively. First white colored L_3, prepared for pupation, were found after 27 days (1 almost white L_3 was found after 19 days in the soil, but not in the pupal chamber). First pupae were found after 35 days. First fully colored adults of the filial generation were found 41 days after the foundation of the brood. It is probable, that under ideal conditions (optimum temperature and moisture, plenty of food) L_1 and L_2 instars together last up to one week, that L_3 last for 15–20 days, and that the pupa develops for ca. 10 days. Hence, the ontogeny from the oviposition to the hatching of new adults will not last much longer than 30 days. [Data from the brood Nr. 2 are not considered here, because the beetles were kept under unsuitable conditions.] I consider *A. fossor* to be a bivoltine species in Central Europe, perhaps having an incomplete third generation (if L_3 or pupae hibernate in addition to adults). The generations are asynchronous: There is an overlap according to local conditions, and – because of the rather rapid ontogeny – also within localities. The reproductive period probably lasts from May to the late August (an unsuccessfull attempt at starting a new brood – Nr. 6 – with adults reared in captivity is not considered significant). I collected adults in the field from the late April to the early October. They strongly preferred cattle dung pads, but time to time were found also in sheep and horse dung pads.

L_1 were found in egg chambers, already somewhat broadened by the feeding activity of the larvae. A substantial proportion of L_1 in the broods Nr. 9a–c (3rd and 4th controls) have already eaten out a tunnel. In most cases, this tunnel was not yet connected with the cavity, formed by adults in the dung pad, but this connection already did exist in a few cases. A single L_1 was found directly in a cavity, measuring 30×25×8 mm. L_2 were found on rather different places (studied in detail in the broods Nr. 9b–c). Some larvae were in closed egg chambers, showing no signs of a tunnel, and their food supply was already almost consumed Some L_2 were in secondary chambers inside of the dung pad, this chamber being isolated, or connected with the respective cavity (recorded also in the brood Nr 5, see Fig 11) Remains of the egg chamber and a tunnel connecting it with the secondary chamber were found in some cases

In the brood Nr 5 (2nd control), one L_1 and one L_2 were found in soil chambers just under the dung pad (Fig 10) The roof of these chambers was formed by the bottom of the dung pad It is rather probable, that eggs were laid in egg chambers, positioned in the soil, not in the dung During the 4th control of the same brood, four L_2 were still found in the same position, while one L_2 was found inside the dung pad

L_3 were found feeding anywhere in the dung pad, incl its upper part In the brood Nr 4, L_3 were found also in the soil under the disintegrated dung pad, in depths of up to 50 mm One of these L_3 was freshly hatched (with exuvia of L_2) Unlike the situation in *A scrutator*, no tunnels between the soil and the dung pad were found here

White-colored L_3 prepared for pupation were found in pupal chambers with smoothed walls, lined with a thin layer of larval droppings

The behavior of *A fossor* females during oviposition is probably similar to the same behavior of *A scrutator* females (see above) The behavior in *A fossor* females, however, seems to be more variable, particularly in respect to the less pronounced tendency to form brood depressions, bottle-shaped burrows, and spherical brood masses, separated from the dung pad by a soil layer The basic difference between the two species is in the duration of their ontogeny, and in the voltinity.

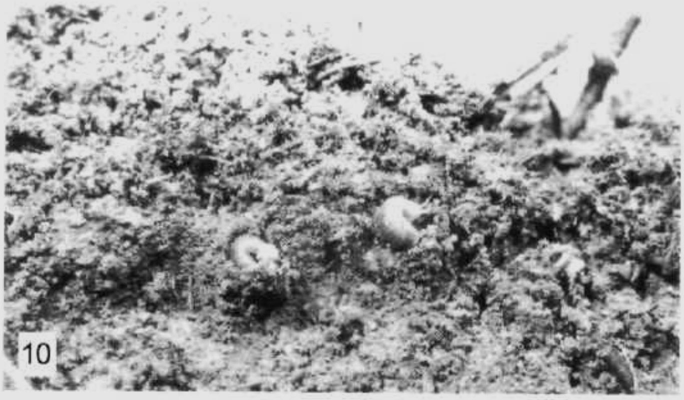
Aphodius (*Colobopterus*) *erraticus* (Linnaeus, 1758)

The formation of brood masses was followed from its beginnings only in broods Nr. 7a–c The position of egg chambers in the soil at the lower end of the brood mass, as well as the shape of brood masses agreed with the data published by Rojewski (1983) However, brood masses (Rojewski calls them "clusters") were thicker, not separated from the dung pad (Fig 12), and placed singly, or in aggregates of two No furcated brood masses were found (cf Rojewski 1983 274) Maximum length of a brood mass was ca 31 mm The eggs were glued to the walls of egg chambers (no details were studied) Their axis was horizontal, or their free end was sligtly elevated Each brood mass was accompanied with only a single egg chamber

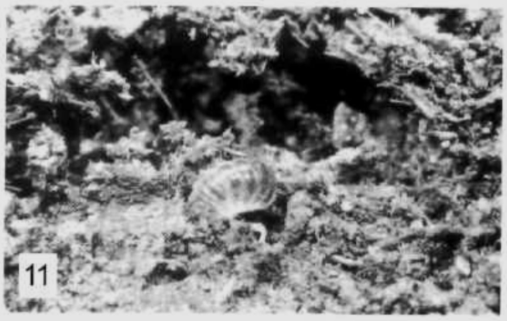
Soil particles formed a solid cover of brood masses in the broods Nr 7a–c This soil cover started to separate from the brood mass during the 3rd control of the brood Nr 7a, forming a space between the cover and the brood mass L_1 and L_2 were already feeeding on the brood mass in that time

L_2 and L_3 were found in the remains of the brood masses up to 50 mm under the dung pad in the broods Nr 3 and 4, respectively It is thus probable, that some brood masses were separated from the dung pad Tunnels between the dung pad and individual brood masses lined with a thin layer of dung, as described by Rojewski (1983), were not observed In the brood Nr 6, some L_2 and L_3 were found in partly consumed brood masses, placed either just under the dung pad, or separated from the dung pad by a soil layer On the other hand, seven L_3 were found feeding directly inside of the dung pad in the brood Nr 2 (Only dung was checked during the 1st control, so that other larvae feeding in brood masses could not be observed) The same applies to some of L_3 in the broods Nr 4 and 8 Some of the latter L_3 were found on remains of brood masses ca 30 mm under the soil surface, so it impossible to say, whether these brood masses were separated from the dung pad One L_2 in the brood Nr 6a was found in a chamber just under the dung pad, feeding directly on the dung pad

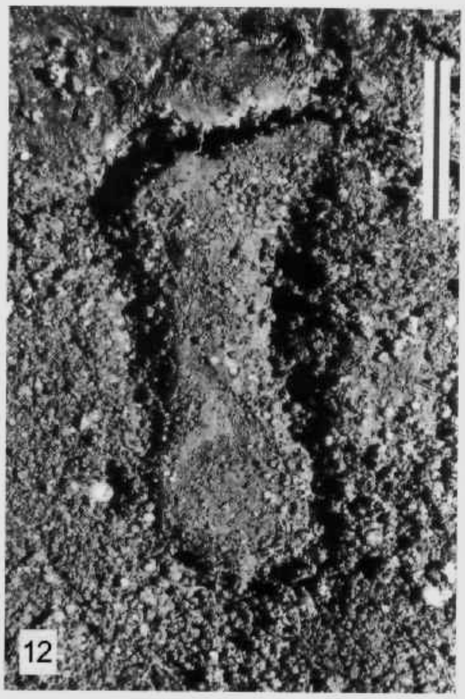
In the brood Nr 8a, behavior of a female during the formation of a brood mass was observed on the 1st and 2nd days after the foundation of the brood She excavated a cavity ca 15–20 mm under



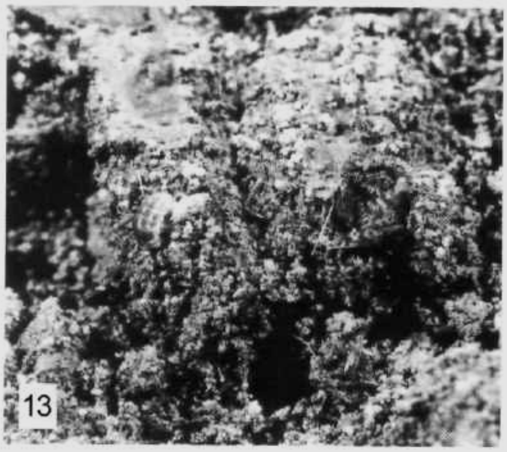
10



11

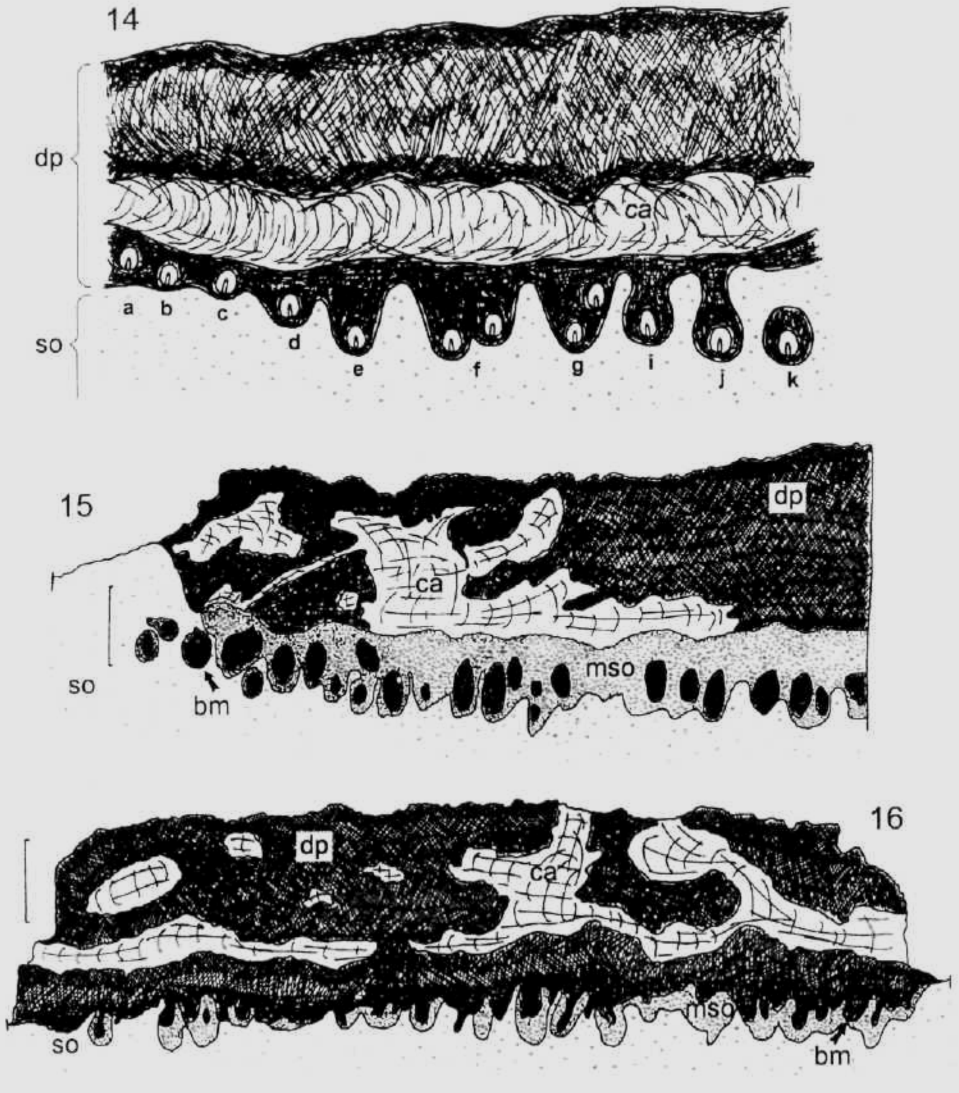


12



13

Figs 10–13. 10–11: *Aphodius fossor* (Herbst). 10 – L_1 (on the left), and L_2 in chambers under the soil surface; 11 – L_2 in a secondary chamber connected with a cavity. 12–13: *A. erraticus* (Herbst); 12 – brood mass with an egg chamber; 13 – two L_2 feeding on brood masses. Scale bar = 10 mm. All photographs by P. Šrůta.



Figs 14–16. 14 – Schema of the oviposition habits of *Aphodius scrutator* (Herbst), and *A. fossor* (Linnaeus). 15–16: Nesting in wooden frames as observed through glass pane, in *A. scrutator* (15), and *A. fossor* (16). a–k – variability of oviposition habits, dp – dung pad, ca – cavity, bm – brood mass, mso – moist soil immediately under the dung pad, so – soil. Scale bar = 20 mm.

the dung pad (for details see Rojewski 1983), but its exact shape could not be seen though the glass pane. No activities of this female leading to the formation of an egg chamber or a brood mass were observed from the 3rd day after the foundation of the brood onwards. Brooding behavior of a female was observed on the 1st day also in the brood Nr. 8b, but no details could be seen. [Sex of these beetles was inferred, because the beetles were not collected and sexed.]

In the field, a brood mass, belonging probably to *A. erraticus*, was found at Lysá nad Labem – Karlov on 22 July 1992. Its diameter was ca. 4 mm, and its depth ca. 14 mm. It was located under a fresh, ca. one day old cattle dung pad, in hard, rammed soil in a corral at a watering place. Axis of the brood mass was approximately perpendicular to the ground. There was no space between the brood mass and the dung pad. An adult individual of *A. erraticus* was found in the soil just under the surface of the ground, ca. 1–2 cm from the upper end of the brood mass. (Its sex was not determined, and its relations to the brood ball were not certain.) No egg chambers were found, although the soil was checked till the depth of ca. 5 cm. Twenty cattle dung pads of approximately similar age were controlled. Together, the following species were found: ca. 150 *Aphodius subterraneus*, ca. 20 *A. fimetarius*, ca. 15 *A. erraticus*, ca. 10 *A. haemorrhoidalis*, 4 *A. fossor*, 2 *Onthophagus fracticornis* (Preyssler, 1790), and 3 *Geotrupes spiniger* (Marsham, 1802).

None of the successfulll broods contained only a single female of the parental generation. It was thus impossible to estimate the fecundity of this species. Nevertheless, 9 larvae were found in the brood Nr. 7a, which consisted of two females. Hence, I concur with Rojewski's (1983) opinion, that a female lays a maximum of ca. 10 eggs.

L_1 were found on the 3–5th day after the foundation of the brood, L_2 on the 5–12th day. (A larva from the brood Nr. 7a, observed on the 3rd day after the foundation of the brood, could be L_2,, but it was only seen through a glass pane, and the number of the instar could not be exactly determined.) Feeding L_3 were observed on the 5–15th day, white L_3 preparing for pupation on the 12––21st day. Pupae were found on the 18–25th day (in the broods Nr. 2a–b, 6b, and 7b), but exceptionally also on the 42–62nd day (brood Nr. 1). Pupal chambers were not lined with a thin layer of dung, their walls being formed by rammed soil, whose texture was clearly visible (3 pupal chambers in the brood Nr. 6b). First teneral adults of the filial generation were seen on the 25th day.

The larvae from all instars were found feeding on the brood mass from outside (detailed observation on the broods Nr. 7a, and 7c; see Fig. 13). They were observed feeding on lower, middle and upper part of the brood mass. Nothing was seen, what could support a view, that the larvae use the brood ball from its lower end towards its upper end. Some L_3 were found on the lower end of the brood mass, while some L_2 on its middle and upper end. Feeding inside of the brood mass was never observed.

The data obtained generally support observations on the behavior of females during the oviposition, and the formation of brood masses and egg chambers first made by Rojewski (1983) and later confirmed by Zunino et al. (1994). However, the observations mentioned above indicate, that the brooding behavior is much more variable: A female is quite probably able to form brood masses, insufficient for the larvae as a food source for their whole ontogeny, or not to build brood masses at all, and position the egg chamber in soil directly under the dung pad, perhaps at a distance from the dung as is the distance between the egg chamber and the brood mass in "standard" cases. A possibility cannot be ruled out, that some females exceptionally create egg chambers on the border between the soil and the dung pad, or even inside the lower layer of the dung pad.

Larval behavior can be summarized as follows: Hatched L_1 reach brood mass (or bottom of the dung pad) by burrowing. The larvae feed on the brood mass from outside, wandering on its whole surface. If a larva consumes the brood mass before finishing its development, it starts to feed on the dung, either on the border between soil and the dung pad, or inside of the dung pad. If no brood mass is available, L_1 migrates directly to the bottom of the dung pad. L_3 finish feeding, and migrate to lower soil layers, where they form their own pupal chambers, not lined with dung, and pupate.

The development of the first two instars lasts together less than 5 days, that of L_3 ca. 10–15 days, and the pupal stage lasts for another ca. 10–15 days. The whole ontogeny from the oviposition to the hatching of adults lasts a maximum of 25 days under optimal conditions. The reproductive activity starts probably in the first half of May, and probably continues till the end of August. [An unsuccessfull brood was founded with adults collected on 20 August 1991 . Four broods were reared in wooden frames and a plastic case, and controlled after 8, 9, and 14 days from their foundation. I do not consider this case as sufficient for excluding August from the breeding season.] I collected adults in the field from the last decade of April till the middle of November. I consider *A erraticus* in Central Europe to be a bi- or trivoltine species. The generations are overlapping, similarly as in *A. fossor*. It is probable, that adults are hibernating, but also white L_3 in pupal chambers, and pupae possibly do that.

Aphodius (*Eupleurus*) *subterraneus* (Linnaeus, 1758)

Only a damaged egg chamber with a dead egg was found inside the dung pad during the first control of the brood Nr. 3. Its exact shape and size were not seen. L_1 were found exclusively inside the dung pad in the broods Nr. 3, 4, and 6. They were found in all layers of the dung pad in the brood Nr. 4. A single L_1 was found in the brood Nr. 6 ca. 5 mm above the bottom of the ca. 30 mm thick dung pad. Only narrow tunnels excavated by adults were found in the latter brood. Unlike in the former three species, no signs of cavities or brood masses were found in this species. The borderline between the soil and the dung pad did not change in the brood of this species, although it was controlled daily through a glass pane. (These are the only controls not listed in the Table 1.) On the basis of these observations, I believe, that the reproductive strategy of *A. subterraneus* does not include nesting behavior.

Oviposition habits were not observed in the field.

Fecundity was not estimated, because each brood included more than one female.

Overall, 86 larvae were found in the brood Nr. 4 during the 1st control: 13 L_3 were in chambers and tunnels in the lower, dense layer of the dung pad (some of them being freshly hatched, still with the exuviae of L_2). 57 L_2 and 16 L_1 were found in all layers of the dung pad. The latter two instars occurred in the uppermost layer in approximately equal numbers, while L_2 were by far more numerous than L_1 in the lowermost layer. This indicates to some degree, that the larvae almost do not migrate though the dung pad until they finish feeding, i.e. that they do not move far from the place, where they hatched. Their development seems to be faster in the lower layer of dung pads, where the living conditions are better than in the upper layer, which dries out and hardens. Nevertheless, it should be kept in mind, that these observations were not done under field conditions, where the asynchronous development in different layers of the same dung pad needs not be a rule, because the beetles have much more diverse choice, where to place their eggs.

In the brood Nr. 4 (3–5th controls), white L_3, pupae, teneral adults, and fully colored adults were found in pupal chambers, located in soil and lined with a 0.5–1 mm thick layer of larval droppings.

Duration of individual instars could not be properly estimated because of the developmental asynchrony mentioned above. The first two instars together probably do not last more than 10 days under ideal conditions (see brood Nr. 6), and the whole ontogeny from the oviposition to hatching of adults of the filial generation is probably only slightly longer than one month.

The reproductive season lasts probably from April to August. [The broods founded on 3 and 16 August 1992 (adults collected at Lysá n. L. – Karlov), respectively, were unsuccessfull, but it is impossible to generalize this observation.] It is possible, that the reproductive season starts and ends earlier than that of *A. erraticus* (see Table 1). In the field, I collected adults of *A. subterraneus* between late March and August, occasionally even in early October. I suppose, that *A. subterraneus* is bivoltine, perhaps trivoltive under suitable conditions in Central Europe, and that adults, and to a lesser degree also perhaps white L_3, and pupae are hibernating.

***Aphodius (Otophorus) haemorrhoidalis* (Linnaeus, 1758)**

The behavior of females during oviposition and the formation of egg chambers were not observed. The oviposition habits were observed only in the brood Nr. 5 (see Fig. 17). Two eggs and five L_1 (incl. one freshly hatched) were found in egg chambers in moist soil just under the dung pad in maximum depths of 3 mm. Another five eggs were found on the bottom of a tunnel excavated by adults in the dung pad, 2–4 mm above the ground. All eggs were glued approximately in a vertical position. The larvae were found only inside the dung pad in all other broods. I believe, that this is a proof of the absence of nesting behavior and formation of brood masses in *A. haemorrhoidalis*.

Oviposition habits were not observed in the field.

All broods included more than one female, so that fecundity was not estimated.

Most L_2 and L_3 were found inside of dung pads, while only two L_3 were found in the soil just under a dung pad. The latter two larvae were found during the 1st control of the brood Nr. 4, which contained at that time 58 L_3. A minority from 30 L_3 were found in the upper layer of the soil during the 2nd control of the brood Nr. 3. However, this was not an original situation, because part of the dung was broken and buried during the 1st control. A single white L_3 prepared for pupation (brood Nr. 3, 2nd control), and two pupae (brood Nr. 1, 2nd control) were found in the soil. It was not the first control, and the situation was not exactly documented, but I assume that L_3 migrate to the soil, and form there their pupal chambers.

During first controls, several different instars were found in most broods, with the exception of the brood Nr 5. This was similar to *A subterraneus*. It is possible that this was caused by laboratory conditions, and that the situation is different in the field (see above under *A. subterraneus*).

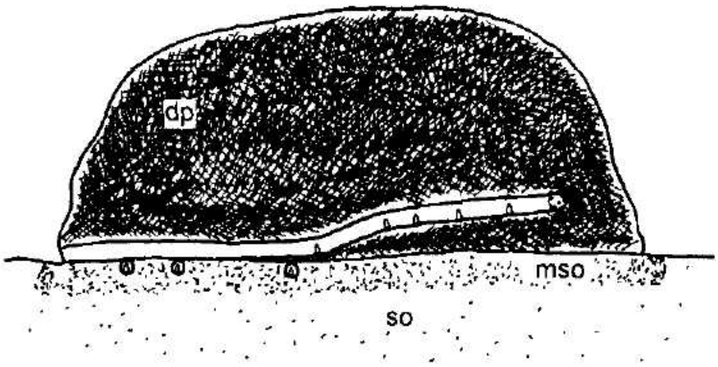


Fig. 17 Schema of the oviposition habits of *Aphodius haemorrhoidalis* (Linnaeus) For symbols see Figs 14–16

The time schedule of the ontogeny can be summarized as follows L_1 and L_2 live maximally one week each I estimate the longevity of L_3 under optimal conditions at 10 days, with 2 weeks as a maximum The whole ontogeny from oviposition to hatching of filial generation lasts slightly over one month

The reproductive season lasts probably from May to August I suppose that this species is bi- or trivoltine in Central Europe, depending on environmental conditions, and that adults, L_3, and pupae are hibernating I collected adults in the field between the last decade of April and September, and occasionally also in the first half of October

DISCUSSION

1. Variability of the oviposition habits

Brooding behavior of adults, and their behavior related to oviposition were studied by previous authors in four out of five species reported on the present paper (first observations of *A subterraneus* are presented here) The data on *A scrutator* were published by Xambeu (1901), Palestrini & Barbero (1994), and Barbero & Palestrini (1995) Reports on *A fossor* were given by Zunino & Barbero (1990), and Zunino (1992) *A erraticus* was studied by Rojewski (1983), and Zunino et al (1994), while the oviposition of *A haemorrhoidalis* by Yoshida & Katakura (1992) After comparing these data, and the data given in the present paper, it is possible to conclude that it is difficult to completely cover the behavioral variability of these beetles

Xambeu (1901) found only spherical brood masses isolated from the dung by a soil layer in *A scrutator* The same observation were made by Zunino and Barbero (Zunino & Barbero 1990, Zunino 1992) in *A fossor* On the other hand, Palestrini and Barbero (Palestrini & Barbero 1994, Barbero & Palestrini 1995) found only brood masses connected with the dung pad (their "cylindrical nest masses") in their broods of *A scrutator* According to my observations, the oviposition habits of *A scrutator* and *A fossor* range from the formation of egg chambers within the dung pad, that lack any signs of the relocation of the dung, to the formation of the above mentioned spherical brood masses

Rojewski (1983) described different shapes and complexes of brood masses in *A erraticus*, incl furcated brood masses, and aggregations of brood masses He found also large brood masses, and relevant egg chambers, forming food resource for up to three larvae Zunino et al (1994) do not mention such a variability Only simple brood masses with a single egg chamber in each were found also in my broods of *A erraticus* In addition, I found that some brood masses do not contain sufficient food for the whole development of the larva, and that it is possible that no brood masses are formed in some cases In the latter case, egg chambers are placed under the dung pad, or perhaps even inside the dung pad (cf Results) This corresponds with the experimental data obtained by Zunino et al (1994), showing that – in the absence of brood masses – the larvae are capable of developing inside of dung pad

Yoshida & Katakura (1992) found egg chambers of *A haemorrhoidalis* in all layers of dung pads, and in the soil under them They observed that most egg chambers were build inside of the dung My observations basically support their data, but I found eggs of this species directly in tunnels excavated by adults, not in egg chambers

Using the data presented above it is possible to conclude that females of *A scrutator* and *A fossor* tend to lower the predation pressure on their eggs and on young larvae by building brood masses as a source of quality food At the same time, the danger of the intraspecific (L_3 and conspecific adults), and interspecific competition is lowered This tendency, realized through the formation of brood masses, seems to be much more pronounced in *A scrutator* (Figs 15–16 show the situation in broods from wooden frames with largest brood masses). This probably corresponds with the longer life of the relatively more vulnerable instars L_1 and L_2 in *A. scrutator* than in *A. fossor*, with the different duration of the whole ontogeny, and with voltinity. A population of the univoltine *A. scrutator* would be more endangered by great losses of eggs and larvae than a population of *A. fossor*, which is probably at least bivoltine. [See also the differences in the orientation of the axis of eggs in egg chambers in these two species. Considering the limited amount of relevant data, and their uncertainty, this aspect is to be accepted with great caution. The same applies to the observations on the behavior of the adults of *A. scrutator*.] The more advanced "nesting behavior" of *A. scrutator* is thus probably an expression of the basic reproductive strategy of this species. Basically, the oviposition habits are similar in these two species.

Whether *A. scrutator* and *A. fossor* lay their eggs in simple egg chambers, depressions of different depth, bottle-shaped burrows or spherical masses separated from the dung pad depends on a number of factors: density, texture and size of the dung pad; density and texture of the soil influencing the ability of adults to burrow, climatic conditions; physiological state of the ovipositing female, the relation between the amount of suitable food sources (dung pads), the number of mature females, and the number of other insects trying to occupy the dung pads; etc. It should be remembered, that the data were obtained under laboratory conditions, not in the field. In spite of that, I believe that both these species (despite some differences described in the previous paragraph) show great plasticity in their oviposition habits (see Figs. 14 and 18). [Certainly, it is possible to assume that populations inhabiting localities with looser soil will more often – or even almost exclusively – lay eggs in nest-like structures, even those shown in Fig. 14k. However, both these species occur on various types of the soil, showing no habitat preferences.] The plasticity of the oviposition habits in these species reflects their broad ecological valency. The same probably applies to *A.* (*Aphodius*) *elegans* Allibert, 1847 (see Hosogi 1985)

The behavior of *A. erraticus* is very different. The females form brood masses, providing with food all larval instars, and the egg chamber is positioned outside of the brood mass. In Rojewski's (1983) broods, the substrate was sandy, i. e. looser than in my experiments. He obtained brood masses with a more variable shape, relatively narrower and longer, and separated from the dung pad, sometimes with more than one egg chamber. [I am not able to decide, whether a vertical tunnel with walls lined with a layer of larval droppings is always present, when the brood mass is separated from the dung pad.] I used rammed soil containing only small admixture of sand in my broods, and I obtained relatively broad and short brood masses, not separated from the dung pad, and always containing only a single egg chamber. I suppose that the oviposition habits (especially the shape of brood masses and their position) of *A. erraticus* are influenced basically by the same factors as those of *A. scrutator* and *A. fossor* (see above).

Unlike in *A. scrutator* and *A. fossor*, I believe that forming brood masses is obligate in *A. erraticus*, and that reduced or absent brood masses are a substitute. [It is possible to assume that the physiological state of females is more important in this species than in *A. scrutator* and *A. fossor*.] I believe, that such a reduced nesting behavior reflects the behavioral plasticity of the species. Nevertheless, it is to be understood as a deviation from the standard reproductive strategy, consisting in the formation of brood masses that provide food for the complete larval development. This is supported also by the feeding habits of the larvae, and their morphological adaptations (see Results, and parts Nr. 3 and 5 of this chapter). The reproductive behavior is roughly similar in *A.* (*Colobopterus*) *quadratus* Reiche, 1847 (Hosogi 1985, Kim & Lumaret 1987, Yoshida & Katakura 1992).

Variations in the position of the egg chamber in *A. haemorrhoidalis*, and probably also in *A. subterraneus*, is probably influenced by factors, mainly external, that are similar to those influencing the oviposition habits in the formerly discussed species. The reproduction is more endangered by predation and competition in these non-nesting species. It is possible to assume, that the occupancy of the dung pad by other insect species play here a more important role.

NOTE. The feeding strategy of adults is probably variable as well. Chromý (1979) observed adult *A. scrutator* excavating in loose loess soil deep and narrow tunnels and filling them with pieces of dung, forming thus cavities in the bottom of the dung pad. [This is not a misidentification with the formation of brood masses. Chromý explicitly mentioned that he observed feeding habits, and that he considers nesting improbable in this species.] The loose loess probably allowed the beetles to hide their food, and save it from desiccation. I found all the studied species of dung beetles most often under the crust of fresh cattle dung pads, or near the periphery under dung pads. On the other hand, dung beetles were found in all places within older, dense dung pads. None of my observations were done on dung pads located on such a loose substrate. This parallel between the feeding and nesting behavior is worth of mentioning, but cannot be generalized, because our knowledge of this topic is insufficient.

Another point that is worth of mentioning is as follows: So far as known, adults of *Aphodius* species, incl. species with a certain degree of nesting behavior, and adults of most of "primitive" nesters from the subfamily Coprinae always feed in dung pads, while those species from the subfamilies Coprinae and Scarabaeinae that have advanced nesting behavior relocate dung into their feeding burrows (cf. Halffter & Matthews 1966, Halffter & Edmonds 1982).

2. The fecundity of females

Zunino (1992) mentioned that females of *A. fossor* lay a maximum of 5–12 eggs, and that they can "repeate [their] nesting cycle several times". My observation that females of *A. scrutator* and *A fossor* can produce at least 50 eggs within a few days is not at variance with Zunino's opinion. It is possible that some unsuitable conditions in the dung pad, in which a female started to lay eggs, can result in the interruption of the oviposition. On the other hand, it is possible that some females interrupt oviposition for (unknown) physiological reasons, and lay eggs in several short cycles This may be a purely individual variability.

Rojewski's (1983) observation that a single female of *A. erraticus* forms a maximum of 10 brood masses was not unequivocally confirmed by my observations, but is probably correct. If the fecundity of the females of *A erraticus* is indeed much lower than that of the females of *A. scrutator* and *A fossor*, then this is another support for the opinion that the reproductive strategy of *A erraticus* markedly differs from that of the remaining studied dung beetle species.

Basically similar, but quantitatively even more pronounced differences between two species representing the two "types" of brooding strategy were found by Yasuda (1987) in *A. elegans* and *A quadratus*. He pointed out, that the fecundity is markedly higher in *A. elegans* than in *A. quadratus*. The fecundity of the latter species is similar to that of *A erraticus*. In addition, Yasuda (1987) found, that egg mass of *A. elegans* is approximately five-times less than that of *A. quadratus*.

3. Larval behavior

A. scrutator and *A fossor*

The main behavioral characteristic of the first two instars of *A. scrutator* and *A. fossor* is the consumption of the brood mass (when it is formed) from inside. Other aspects of their behavior are variable. Some L_1 were found that did not eat up their brood mass yet, but that already formed a tunnel, sometimes even connected with the cavity excavated by adults. In broods with obligate brood masses, where egg chambers were only exceptionally found inside of the dung pad, some L_2

were observed feeding in the same dung layer as L_3 On the other hand, some L_2 were found in almost consumed brood masses without any signs of a tunnell It was not discovered what is the reason for this variability It can be speculated, that the following factors may influence it environmental conditions, particularly desiccation of the soil and the dung and related changes in the quality of food of the larvae, distance between egg chamber and the cavity, and – because I assume advanced territorial behavior of the larvae – also the distances between individual egg chambers [Larvae collected from brooding cases and brought together were very aggressive to each other]

It is highly probable that most larvae migrate from brood masses into the dung pad during the 2nd instar The main factor influencing this behavior is probably food shortage (brood ball is consumed), or the fact that dung pad provides food of better quality than the remaining part of the brood mass It can be assumed, that this behavior is influenced by the competition between the larvae (see above) that come nearer to each other during the consumption of their brood balls Cavities formed by females during the building of brood balls probably accelerate the rate of larval dispersion These cavities are obligatorily present in the vicinity of egg chambers It is thus necessary to accept the possibility that they are not formed just because of the translocation of the dung used to build a brood mass, but that they are part of the overall reproductive strategy of *A fossor*, and especially of *A scrutator*

L_3 are foraging within dung pads They were found both in secondary chambers, and without any chambers Over time, dung pads were consumed by the larvae (especially their lower layer), and the larvae were found in vertical tunnels connecting upper soil layer with the upper dung layer These observations were made under laboratory conditions, where the food sources were limited, and the dung was not covered with a crust It is possible to assume that under natural conditions parts of dung pads remain less disturbed in some cases, and that L_3 remain in chambers till the end of their feeding activity Nevertheless, it is clear that they are able to react to changing conditions by migrating within the dung pad in both vertical and horizontal direction, and also by vertical migration between the dung pad and the soil Whether is the building of vertical tunnels by L_3 under natural conditions a rule, or not, cannot be decided on the basis of available data

Lining of pupal chambers with a layer of dung by L_3 was observed in *A fossor* Life habits of the larvae of *A scrutator* are similar to those of *A fossor*, so that I assume that this behavior is present also in this species

A erraticus

The basic characteristic of the larvae of *A erraticus* is the consumption of the brood mass from ouside, not from inside This is similar to the behavior of the larvae of *A quadratus* (Hosogi 1985) Larvae probably migrate over the whole brood mass L_1 are partly protected by a soil crust covering the brood mass (see Results) Both migration and feeding activity are not regular – remains of brood masses found under laboratory conditions with L_3 were irregularly and not uniformly shaped The migration of the larvae may be influenced to some degree by changing quality of the food (desiccation?), but the data are too scanty to allow for a more exact explanation It is possible that the larvae repair cracks appearing in the brood mass (see part Nr 5 of this chapter)

The pupal chamber is not lined with a layer of dung by L_3 (see also Rojewski 1983) In this respect, *A erraticus* differs from *A fossor, A subterraneus*, and probably also from *A scrutator* and *A haemorrhoidalis* This combination of relatively "advanced" brood mass, and relatively "primitive" pupal chamber is unique among the studied species

A subterraneus and *A haemorrhoidalis*

The larvae of both these species were found in different layers of the dung pad The usually fed (incl L_3) in clearly separated chambers It is possible, that some of them feed on the border between the soil and the dung pad (see observations on *A haemorrhoidalis* in Results, and in the 1st part of this chapter) It is probable, that these larvae do not migrate through the dung pad This is supported also by the fact that they belong to non-nesting species However, it cannot be expected that L_3 differ in this respect from the L_3 of *A scrutator* and *A fossor* The larvae of *A subterraneus* and the more the larvae of *A haemorrhoidalis* are much smaller than the larvae of *A scrutator* and *A fossor*, and their living conditions under laboratory conditions thus could be closer to the natural conditions, at least in regard to the relative amount of food Small larvae were not forced to migrate, because they had enough food

I observed that the pupal chambers of *A subterraneus* were lined with a layer of larval droppings I suppose that the same is true for *A haemorrhoidalis* – life habits of the larvae are similar in both species, their pupae are small, and are thus more susceptible to desiccation These species commonly occur on localities with heavy soil, that does not allow the larvae to build their pupal chambers in greater depths

NOTE The behavior of the larvae of the genus *Aphodius* is probably more diverse and complicated than expected on the basis of the scarce published data This is indicated e g by the observations on the larval behavior of *A (Amidorus) obscurus* (Fabricius, 1792), and *A (Acrossus) luridus* (Fabricius, 1775), presented by Lumaret & Stiernet (1991) and Lumaret (1983), respectively

4. Seasonal dynamics of reproduction

Adults of all studied species (but *A scrutator* – see Results) occur in Central Europe from the spring to the fall, having maximum densities in the warmest part of the year, i e between May and August Rather few data on the seasonal dynamics of the occurrence, reproduction, duration of the ontogenetic development, and the number of generations per year were published Some of these publications are rather laconic (Landin 1961 209–210) In other papers, only separated populations were studied (e g Schmidt 1935 324, 340, Holter 1982, Yoshida & Katakura 1985) Detailed studies from different part of the area of individual species are missing It is thus impossible to properly compare the effects of environmental factors on the species, particularly daily and seasonal changes of temperature, and the amount and seasonal distribution of precipitation

Also my data from laboratory broods are rather incomplete Nevertheless, they indicate that *A scrutator* is univoltine in Central Europe, while the other four species are at least bivoltine Successfull broods were based on adults collected in the course of 3–5 months (see Table 1)

I suppose, that the seasonal dynamics of reproduction in *A fossor*, *A erraticus*, *A subterraneus*, and *A haemorrhoidalis* is rather variable both geographically and locally The same is true, when the dynamics at a single locality is compared between years (particularly if the weather was different) In addition, there is individual variability within populations, and within seasons (see also Results) I believe, that similar plasticity of the seasonality of reproduction can be found also in a number of other "summer" species inhabiting the temperate zone

5. Oviposition habits and morphological adaptations of the larvae from the systematic point of view

The females of *A scrutator* and *A fossor* obligatorily form egg chambers in simple brood masses The brood masses are either located in a dung pad (cylindrical depression), or are isolated from the dung pad by a soil layer (spherical mass) The fecundity of females is rather high L_1, and to some degree also L_2 develop within brood masses L_3 are feeding in the dung pad, and then migrate into the soil, where they form pupal chambers lined with a thin layer of their own droppings No morphological structures were found on the larvae of these two species, that could be interpreted as an adaptation to the life in a nest (Madle 1935, 1936, Emden 1941, Medvedev 1952, Jerath 1960, Barbero & Palestrini 1995, Vitner 1996) The same applies to *A elegans* (see Hosogi 1985, Kim & Lumaret 1986, Yasuda 1987, Yoshida & Katakura 1992) Their external morphology is not markedly different from the larval morphology of those species, in which the nesting behavior was not observed (incl *A subterraneus*, and *A haemorrhoidalis*) This observation is confirmed on the larvae of more than 50 European *Aphodius* species, incl L_1 of ca 40 species from my own broods (Vitner 1996)

The oviposition habits of *A scrutator* and *A fossor* are rather variable (see Results and the 1st part of this chapter) This fact, and the absence of morphological adaptations allow for the following conclusion The data on the reproduction, ontogeny, and larval morphology of species with oviposition habits of the "type" represented by *A scrutator, A fossor* and *A elegans**) cannot be currently used in classifying individual species in subgenera, or in solving problems related to the subgeneric classification of the genus *Aphodius* [Cf also descriptions of larvae of other three species of the subgenus *Aphodius* by Madle (1935, 1936), Medvedev (1952), Jerath (1960), Barbero & Palestrini (1993), and Vitner (1996), and the data on the larval morphology and oviposition habits of *A (Teuchestes) brachysomus* Solsky, 1874 presented by Kim & Lumaret (1988), and Yoshida & Katakura (1992)]

The females of *A erraticus* obligatorily build stick-shaped brood masses Egg chambers are located in the soil, outside of brood masses The fecundity of females is rather low The brood mass provides food for all three larval instars [Females of *A erraticus* can form brood masses able to provide food for more than one larva (Rojewski 1983) This is not yet confirmed for *A quadratus* See also the 6th part of this chapter] The larvae feed on the brood mass from outside L_3 migrate to the soil after finishing feeding, and build there pupal chambers not lined with their droppings The same applies to *A quadratus* (Hosogi 1985, Yasuda 1987, Yoshida & Katakura 1992) This "type" of the oviposition habits is more clearly characterized than the previous "type" The structure of the pupal chamber indicates that the larvae have a different etho-physiological adaptation

The larvae of *A erraticus* and *A quadratus* posses morphological structures unknown in other species of the genus *Aphodius* marked protuberances on the postclypeus, and modified anal lobes (see Emden 1941, Jerath 1960, Kim & Lumaret 1987, Frolov 1994, Vitner 1996) Their mandibles are slender, whereas those of *A scrutator, A fossor*, and *A elegans* are robust The postclypeal protuberances are probably an adaptation to the locomotion in soil on the surface of the brood mass Anal lobes resemble those of the Geotrupinae, Scarabaeinae, and Coprinae in shape (see e g Medvedev 1952, Ritcher 1966) It is possible, that these larvae repair cracks in the brood mass using anal lobes from outside, while the larvae of the representatives of other subfamilies do this from inside The differences in the mechanics of mandibles in the two groups of species (*A scrutator A fossor*, and *A elegans* vs *A erraticus*, and *A quadratus*) remain unknown, and I am not able to find any explanation for them

I consider the use of the data on life habits and larval morphology in systematics possible They clearly indicate, that *A erraticus* and *A quadratus* are closely related to each other, and that the subgenus *Colobopterus* Mulsant, 1842 in the sense of Dellacasa (1986) is at least partly a natural group However, insufficient knowledge of life habits and larval morphology of the species from the genus *Aphodius*, and of the whole Scarabaeoidea should be kept in mind, and any conclusions should evaluated circumspectly

---

*) This is the only species with known nesting behavior, that does not belong to the group of the subgenera with large scutellum

NOTE. I did not consider here the uncertain report by Jerath & Unny (1965), stating that the "larvae of five species were collected in small dung cells usually about 3–6 inches deep in the soil under dung." The species were *Aphodius (Blackburneus) detruncatus* Schmidt, 1908, *A. (B.) novus* Schmidt, 1911, *A. (Calocolobopterus) senegalensis* Klug, 1835, *A. (Neocolobopterus) maculicollis* Reiche, 1847, and *Didactylia venalis* Schmidt, 1911. In view of the climatic conditions (Nigeria), I suppose, that this were probably cases of cleptoparasitism in telocoprid nests of small-sized Coprinae.

6. On the evolution of the oviposition habits in the genus *Aphodius*

Numerous papers were published on the nesting and reproduction of the representatives of the subfamilies Scarabaeinae, Coprinae, and Geotrupinae, incl. two monographs (Halffter & Matthews 1966, Halffter & Edmonds 1982). On the other hand, the reproductive behavior of the Aphodiinae is less known. The only generalizing synthesis was presented by Yoshida & Katakura (1992). They discerned four types of oviposition habits of *Aphodius* species: Type I – egg chamber in the dung pad (*A. brachysomus, A. haemorrhoidalis, A. (Agrillinus) breviusculus* Motschulsky, 1866, and *A. (Agrillinus) pratensis* Nomura et Nakane, 1951); Type II – egg chamber in the soil under dung pad, without brood mass (*A. (Bodilus) sordidus* (Fabricius, 1775), *A. (Phaeaphodius) rectus* Motschulsky, 1866, and *A. (Phalacronothus) pusillus* (Herbst, 1789)); Type III – egg chamber in a small brood mass, providing food for L_1, and partly for L_2 ["second and third instars eat freely in droppings on the soil" (Yoshida & Katakura 1992: 6)] (*A. elegans*); Type IV – egg chamber in the soil near the lower end of the brood mass [There are exceptions – "Larvae ... can complete the growth ... in the unburied dung (third instars; ...)" (Yoshida & Katakura 1992: 6)] (*A. quadratus*). They treated these types as distinct units and suggested the following evolutionary relationships: Types I and II are ancestral, and they could evolve from one another. Type III could evolve from Type I or Type II. Type IV evolved from Type II. The evolution of Types III and IV was independent. The authors supported this mainly by stating that brood mass is formed first, and then the egg is laid in Type III, while the egg chamber is formed first and the egg is laid, and only then the brood mass is formed in Type IV. They consider Types III and IV analogous to some oviposition habits of burrowers from the subfamilies Scarabaeinae and Geotrupinae (for details see Yoshida & Katakura 1992: 6). They conclude that the genus *Aphodius* is suitable for studying the problem of the evolutionary origins of brood caring habits of the coprophagous Scarabaeoidea because it contains both non-nesting species, and species showing some brood care.

The results presented here (see Results, and the 1st part of this chapter), and the data in Yoshida & Katakura (1992: 2) indicate, that the classification of the oviposition habits by the latter two authors is somewhat discussible. Egg position is variable in most of non-nesting species they studied: Egg chambers were found in different dung layers and in the upper soil layer (see also the data on *A. haemorrhoidalis* in the Results section of this paper). Hence, Type I and Type II cannot be clearly discerned. Variations between "nesting" and "non-nesting" oviposition habits were found in the "nesting" species *A. scrutator*, and especially in *A. fossor*. I think that it is possible that these two species and *A. elegans* exceptionally build egg chambers on the border between the soil and the dung pad or in the uppermost soil layer under the dung pad. (I am not able to find a hypothetical explanation for this, perhaps stress factors during the oviposition could play a role here.) It is also possible to assume on the basis of my own and published results (Yoshida & Katakura 1992, Zunino et al. 1994) that a similar variability is present – though to a smaller degree – also in the oviposition habits of *A. quadratus*, and *A. erraticus*. Hence, these "nesting" species always can use oviposition habits of at least two "Types", this being confirmed for *A. fossor*, and *A. scrutator*, while it is very probable for all other species. It is thus impossible to discern Type I (and possibly Type II) from Type III of the oviposition habits sensu Yoshida & Katakura (1992). Similarly, it is not possible to discern Type II (and perhaps Type I) from Type IV. This somewhat lowers the usability of the schema of evolutionary relationships among the types of oviposition habits as presented by Yoshida & Katakura (1992), because it is not possible to treat their "Types" as discrete units, this being particularly clear for Types I, II, and III. Nevertheless, the two main tendencies of the evolution of the oviposition habits in the genus *Aphodius* presented by Yoshida & Katakura (1992) are correct.

I present here a modified hypothetical schema of the evolution of the oviposition habits in the genus *Aphodius* (see also Fig. 18).

The oviposition habits of non-nesting species are ancestral. The position of the egg chamber is intraspecifically variable, being anywhere in the dung pad, in the uppermost soil layer, or in tunnels excavated by insects inhabiting the dung pad. The position probably depends on environmental conditions.

I discern the following two tendencies of the evolution of the oviposition habits:

1) A tendency leading to the removal of the offspring in the early stages of ontogeny from the zone of direct predation and competition, and – at the same time – leading to the provisioning of the first (or even the second) instar with food in the form of a brood mass, i.e. to Type III in the sense of Yoshida & Katakura (1992). An extreme case is a brood mass, fully separated from the dung pad by a soil layer. I believe, that advantage of being safe in the early stages of ontogeny and the advantage of being provided with food are comparable. I think it is possible that this tendency is reversible – non-nesting position of the egg chamber is still present in the pattern of the reproductive strategy of these species, although this is a less common case. This tendency is represented by

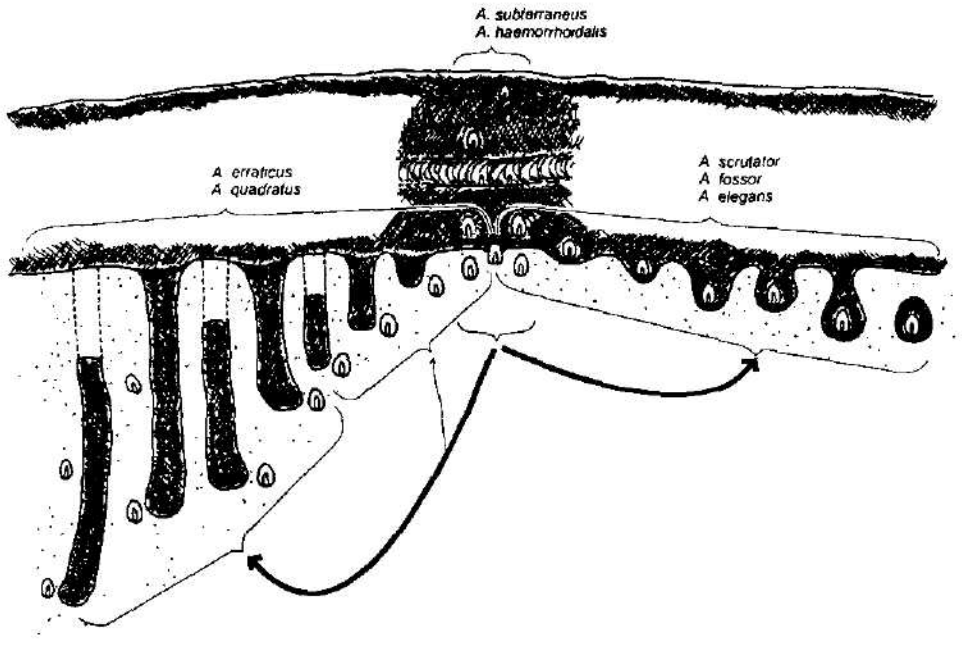


Fig. 18. Hypothetical schema of the evolution trends of the oviposition habits in the genus *Aphodius* Illiger.

A. scrutator, A. fossor, and *A. elegans*. The larvae of these species feed inside of brood masses or inside of dung pad. They do not possess any special morphological adaptations to the life in the nest. Their pupal chambers are probably always lined with a thin layer of larval droppings.

2) A tendency leading to the removal of the offspring from the dung pad and to providing food for their complete development (not without exception) in the form of a sufficiently large brood mass, i.e. to the Type IV in the sense of Yoshida & Katakura (1992). Food provisioning of the larvae plays here a more important role. It is probable that this tendency is irreversible, although the females are still able to form brood masses too small for providing food for the complete development of the larvae if the conditions are not suitable, and that such a situation is nor fatal to the larvae. On the other hand, it is possible that the variability of large brood masses with more than one chamber is discontinuous, because these brood masses are sufficient for two or three larvae, not for "1 1/3" or "1 2/3" larvae. In such a situation, larval aggressivity could be eliminated by an appropriate shape of the brood mass and by appropriate spacing of egg chambers. This tendency is represented by *A. erraticus* and *A. quadratus*. Larvae of these species feed on the brood mass from outside. This behavior is unknown in other nesting species of the coprophagous Scarabaeoidea. Larvae of these two *Aphodius* species have special morphological adaptations. The walls of the pupal chambers are probably never lined with a layer of larval droppings.

Tendency Nr. 2 leads to a more distinctive reproductive strategy than the tendency Nr. 1. In addition to the features presented above, this is supported by the data on the egg mass and the fecundity of females (Rojewski 1983, Yasuda 1987, see also Results, and the 2nd part of this chapter).

It should be remembered, that the oviposition habits of *Aphodius* species are more variable than is the more evolved behavior of the representatives of other subfamilies of the Scarabaeoidea. It cannot be excluded, that there are more tendencies in the evolution of the oviposition habits in the genus *Aphodius* than known so far, and that e.g. some species build simple nests similar to those of the "primitive" burrowers from the subfamily Coprinae ("Pattern I" in the sense of Halffter & Edmonds 1982), in which individuals develop from the egg till hatching of adults. Nevertheless, I assume that the reproductive strategy of most *Aphodius* species is based on their adaptability and the ability to use for reproduction dung pads as they are (perhaps with numerous modifications of behavior, leading to the evolution of nest-like oviposition habits), not on their ability to evolve towards building more advanced nests.

From the methodological point of view I am absolutely convinced that it is impossible to classify the oviposition habits of *Aphodius* species typologically. This would be incorrect, I think, even if much more would be known on the reproductive behavior of *Aphodius* species. It is probable that studying the reproductive behavior of the coprophagous Aphodiinae will face different problems than studying this behavior in other subfamilies of the Scarabaeoidea: relatively simple oviposition habits, and the necessity to follow large variability depending on small changes of environmental factors. [It is probable that studies of the intraspecific variability of the reproductive biology will be more important even in subfamilies with advanced oviposition habits. This is indicated by the observation that the variability of the oviposition habits is variable in some burrowers (e.g. Rougon & Rougon 1982), and by the discovery that a single species is able to use both basic nesting strategies, i.e. burrowing and ball-rolling (see Sato 1997).]

I agree with Yoshida & Katakura (1992) that it is possible to see analogies between the nests of the Geotrupinae and Coprinae and the nest-like structures of *Aphodius* species. Nevertheless, it is necessary to expect that a fundamental difference is present here, indicating that we deal with two qualitatively different adaptations: the larvae of *Aphodius* species do not spend their whole life in brood masses, while the development proceeds from the eggs to adults within brood masses in the former two subfamilies. It is difficult to say, whether *Aphodius* species are more suitable for the study of the evolutionary origins of brood caring habits than representatives of other coprophagous groups of the Scarabaeoidea. They can certainly supply numerous data helping to clarify the evolution of some "primitive" nesting habits. Nevertheless, I think that it is uncertain whether these studies can significantly contribute to our understanding of the origins of advanced nesting habits in the coprophagous Scarabaeoidea in which the process was perhaps less continuous, evolving as a sequence of larger discontinuous steps.

Note It is an open question, when to use the terms, such as "nesting", "nest", "nesting biology", "brood mass", etc. So far as known, the beetles leave nests as adults in other subfamilies, while only larvae develop (completely or partly) in the "nest" or "brood mass" in *Aphodius* species. On the other hand, also a closed egg chamber in a dung pad or in the soil can be understood as a "nest", unlike such cases, when the eggs are laid e.g. in tunnels in the dung pad, excavated by adults of any species, but not by parents with the aim at forming a nesting place. I believe, that these questions are not important from the point of view of studies of the oviposition habits in the genus *Aphodius*. So far, our knowledge is so limited, that the appearance of a terminological chaos does not menace.

SUMMARY

1. It was confirmed that *A scrutator, A. fossor*, and *A. erraticus* form brood masses as a part of their reproductive behavior. The oviposition habits are variable in the former two species, ranging from egg chambers within dung pads to brood masses separated from the dung pad by a soil layer The tendency to build nest-like structures is probably more pronounced in *A. scrutator* than in *A fossor* The oviposition habits of *A. erraticus* are more clear-cut. The absence of brood mass is less common, and probably reflects markedly unsuitable conditions during the oviposition.
2. *A. scrutator* and *A. fossor* build egg chambers within brood mass. The larva feeds on it from inside, leaving it usually in the course of the 2nd instar. Its feeding continues inside of the dung pad. *A erraticus* places its egg chambers in the soil outside of the brood mass, that usually serves as a food source for the larva during its whole life. The larva feeds on the brood mass from outside. After finishing feeding, L_3 of all the three species migrate downwards in the soil, and construct there their pupal chambers. The larvae of *A. fossor*, and probably also of *A. scrutator* line the walls of their pupal chamber by a thin layer of their own droppings. Pupal chambers of *A. erraticus* are not lined with larval droppings.
3. It was found, that *A haemorrhoidalis*, and *A subterraneus* do not build brood masses, and show nor signs of nesting behavior. Pupal chambers of *A. subterraneus* are lined with larval droppings.
4. It was found, that females of *A. scrutator*, and *A. fossor* are able to lay at least 50 eggs each. My own observations indicate, that the published data on a much lower fecundity of the females of *A. erraticus* (ca. 10 eggs) are correct.
5. Uncertain indications were obtained, that subsocial behavior is perhaps developed in *A. scrutator*, manifested in aggressivity during the interspecific competition.
6. It was found, that *A. scrutator* is strictly univoltine in Central Europe, with L_3 hibernating. The remaining four studied species are probably at least bivoltine in this region, showing highly probably both local and intrapopulation variability.
7. An assumption was formulated, that the stronger tendency towards building nest-like constructions in *A. scrutator* than in *A. fossor* is related to the differences in the duration of the first two larval instars, and in the voltinity of the two species.

8. Relations between the reproductive biology of *A. erraticus* and *A. quadratus*, and the morphological adaptations of their larvae were pointed out. The adaptations include: postclypeal protuberances, shape of mandibles, and shape of anal lobes. These adaptations may be used in the systematics, and prove that at least a part of the subgenus *Colobopterus* is a natural group of species.
9. A modified schema of the evolution of the oviposition habits in the genus *Aphodius* was proposed (cf. point Nr. 1): In the ancestral situation, no brood masses are formed, and egg chambers are placed either in a dung pad, or in the soil. An evolutionary trend is represented by species, whose oviposition habits are variable, ranging from the formation of egg chambers without brood mass to the formation of brood masses, that provide food for L_1, and to some degree to L_2 (*A. scrutator, A. fossor, A. elegans*). The other trend leads to the formation of brood masses, that provide food for all three larval instars (*A. erraticus, A. quadratus*). The oviposition habits are less variable here. It is preferred not to discern distinct evolutionary types of oviposition habits, to abandon the typological approach, and to focus on the evolutionary tendencies in studying these aspects of the reproductive biology of *Aphodius* species.
10. An assumption is formulated, that researchers will face other problems in studying brooding behavior in *Aphodius* species, than in studying this behavior in the representatives of the other subfamilies of the coprophagous Scarabaeoidea. The oviposition habits are more simple in *Aphodius* species, but it is more difficult to discern their fine differences, and to interprete their variability.

Acknowledgements

Věra Vitnerová (Čelákovice, Czech Republic) helped me to rear the beetles. Markéta Nejedlá scanned and subsequently designed figures and helped to edit the table Jan Hubert read an earlier version of the manuscript, contributed valuable comments, and helped to computerize the appendices. David Král supplied some beetles, read an earlier version of the manuscript, and contributed valuable comments The photographic credit is due to Pavel Šrůta (all from Praha) I am obliged to all of the named persons

REFERENCES

BARBERO E & PALESTRINI C 1993 [Morphology of the preimaginal stages of Aphodius (s str) foetidus (Herbst, 1783) (Coleoptera. Scarabaeoidae Aphodiinae)] *Lambilloinea* **93**: 143–151 (in Italian, English abstr)

BARBERO E & PALESTRINI C 1995. [Aphodius (Coprimorphus) scrutator description of the larva and notes on its reproductive biology (Coleoptera, Scarabaeoidea, Aphodiidae)] *Fragm. Entomol.* **26** 341–352 (in Italian, English abstr.)

CHROMY J 1979 [Note on the bionomy of Scarabaeidae]. *Zpr. Čs Společ. Entomol. ČSAV* **15**. 37–46 (in Czech)

DELLACASA G 1986 A world-wide revision of Aphodius sharing a large scutellum *Frustula Entomol. N S* **7–8** (20–21)(1984-1985) 173–282

DELLACASA M 1988. Contribution to a world-wide catalogue of Aegialiidae, Aphodiidae, Aulonocnemidae, Termitotrogidae (Coleoptera Scarabaeoidea). *Mem Soc Entomol. Ital.* **66** (1987) 3–455.

EMDEN F I van 1941· Larvae of British beetles II. A key to the British Lamellicornia larvae. *Entomol. Month. Mag.* **77**. 117–127, 181–192.

FABRE J H 1897 *Souvenirs entomologiques Cinquième série* Paris Delagrave, 355 pp

FABRE J H 1899 *Souvenirs entomologiques. Sixième série* Paris Delagrave, 418 pp.

FROLOV A. V 1994. [On the larval morphology of two species of Aphodius (Coleoptera, Scarabaeidae)]. *Zool. Zh.* **37** 103–110 (in Russian, English abstr)

HALFFTER G. & EDMONDS W D 1982. *The nesting behaviour of dung beetles (Scarabaeinae) An ecological and evolutive approach* México: Instituto de Ecología, 176 pp.

HALFFTER G & MATTHEWS E. G 1966: The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae) *Fol Entomol. Mex.* **12–14**: 1–312

HOLTER P 1982 Resource utilization and local coexistence in a guild of scarabaeid dung beetles (Aphodius spp.). *Oikos* **39**· 213–227

Hosogi Y 1985 Ecological studies on the utilization of main coprophagous beetles at pastures in the warm area of Japan *Bull Kochi Prefectural Livestock Experiment Station* **14** 1–152 (in Japanese, English summary)

Jerath M L 1960 Notes on larvae of nine genera of Aphodiinae in the United States (Coleoptera Scarabaeidae) *Proc U S Natl Mus* **111** 43–94

Jerath M L & Unny K L 1965 Larvae of six species of genus Aphodius from Eastern Nigeria (Coleoptera Scarabaeidae) *Coleopterol Bull* **19** 91-95

Kim J I & Lumaret J -P 1986 Contribution à l'etude des Aphodiidae de Coree Description des larves de quatre especes d'Aphodius (Coleoptera, Scarabaeoidea) *Nouv Rev Entomol (N S)* **3** 485–496

Kim J I & Lumaret J -P 1987 Troisième contribution à l'etude des Aphodiidae de Coree redescription de la larve d'Aphodius apicalis Har *Bull Soc Entomol Fr* **91** 171–176

Kim J I & Lumaret J -P 1988 Deuxieme contribution a l'etude des Aphodiidae de Coree (Coleoptera, Scarabaeoidea) *Nouv Rev Entomol (N S)* **5** 159–172

Kral D *1993* Scarabaeoidea Pp 66–71 In Jelínek *J* (ed) Check-list of Czechoslovak insects IV (Coleoptera) *Fol Heyrovskyana* Suppl **1** 3–172

Landin B O 1961 Ecological studies on dung-beetles *Opusc Entomol* Suppl **19** 1–227

Lengerken H von 1954 *Die Brutfürsorge- und Brutpflegeinstinkte der Kafer 2 Aufl* Leipzig Akademische Verlagsgesellschaft Geest & Portig K -G , 383 *pp*

Lumaret J -P 1983 La nidification des Trox (Col Scarabaeoidea Trogidae) *Bull Soc Entomol Fr* **88** 594–596

Lumaret J -P & Stiernet N 1991 Chapter **14** Montane dung beetles Pp 242–254 In Hanski I & Cambefort Y (eds) *Dung beetle ecology* Princeton Princeton Univ Press, 481 pp

Madle H 1935, 1936 Die Larven der Gattung Aphodius I, II *Arb Physiol Angew Entomol Berlin-Dahlem* **2** 289–304, **3** 1–20

Medvedev S I 1952 *Lichinki plastinchatousykh zhukov fauny SSSR Opredeliteli po faune SSSR 47* [*Larvae of Scarabaeoidea of the Soviet Union Keys to the identification of the fauna of the USSR 47*] Moskva/Leningrad Izd Akad Nauk SSSR, 242 pp (in Russian)

Palestrini C & Barbero E 1994 The reproductive biology of Aphodius (Coprimorphus) scrutator (Herbst, 1789) (Coleoptera Scarabaeidae, Aphodiinae) some experimental data *Boll Zool* Suppl 60

Prasse J 1957 Die Entwicklung der Pillenwalzer Sisyphus schaefferi L und Gymnopleurus geoffroyi Fuess in der Brutbirne *Wiss Ztschr Univ Halle Math -Naturwiss* **6** 1033–1044

Ritcher P O 1966 *White grubs and their allies A study of North American scarabaeoid larvae Oregon state monographs Studies in entomology Nr 4* Corvallis Oregon State Univ Press, 219 pp

Rojewski C 1983 Observations on the nesting behaviour of Aphodius erraticus (L)(Coleoptera, Scarabaeidae) *Pol Pismo Entomol* **35** 271–279

Rougon D & Rougon C *1982* *Nesting strategies of three species of coprophagous* Scarabaeinae in the Sahel region of Niger Pp 147–150 In Halffter G & Edmonds W D 1982 *The nesting behaviour of dung beetles (Scarabaeinae) An ecological and evolutive approach* Mexico Instituto de Ecologia, 176 pp

Sato H 1997 Two nesting behaviours and life history of a subsocial African **dung-rolling beetle, Scarabaeus** catenatus (Coleoptera Scarabaeidae) *J Natur Hist* **31** 457–469

Schmidt G 1935 Beitrage zur Biologie der Aphodiinae (Coleoptera, Scarabaeidae) *Stettin Entomol Ztg* **96** 293–350

Vitner J 1996 *Larvy středoevropských druhů podčeledi Aphodiinae (Coleoptera Scarabaeidae)* [*Larvae of the Central European Aphodiinae (Coleoptera Scarabaeidae)*] Unpubl diss thesis Prague Charles Univ , 269 pp (in Czech)

Xambeu V 1901 Moeurs et metamorphoses des insectes 9ᵉ memoire *Rev Entomol* **20** 7–65

Yasuda H 1987 Reproductive properties of two sympatric dung beetles, Aphodius haroldianus and Aphodius elegans *Res Popul Ecol* **29** 179–187

Yoshida N & Katakura H 1985 Life cycles of Aphodius dung beetles (Scarabaeidae, Coleoptera) in Sapporo, Northern Japan *Environ Sci Hokkaido* **8** 209–229

Yoshida N & Katakura H 1992 Evolution of oviposition habits in Aphodius dung beetles (Coleoptera Scarabaeidae) *Pan-Pacif Entomol* **68** 1–7

Zeleny *J 1972* [Entwurf einer Gliederung der Tschechoslowakei für Zwecke der faunistischen Forschung] *Zpr Čs Spolec Entomol ČSAV* **8** 3–16 (in Czech, German abstr)

Zunino M 1992 Food relocation behaviour Pp 297-314 In Zunino M , Belles X & Blas M (eds) (1991) *Advances in coleopterology* Barcelona Eur Assoc Coleopterol , 323 pp

Zunino M & Barbero E 1990 Food relocation and the reproductive biology of Aphodius fossor (L) (Coleoptera Scarabaeidae Aphodiinae) *Ethol Ecol & Evol* **2** 334

Zunino M Canino L & Coletta E 1994 Feeding and nesting behaviour of Aphodius (Colobopterus) erraticus (L) (Coleoptera Scarabaeidae Aphodiinae) *Ethol Ecol & Evol* **6** 451–452

INSTRUCTIONS TO AUTHORS

Acta Societatis Zoologicae Bohemicae publishes in English, original papers on general, applied and systematic zoology, biographies and book reviews Papers by members of the Czech Zoological Society are prefered It is understood that manuscripts submitted are not offered to any other journal for prior or simultaneous publication

Authors of taxonomic papers must respect the articles of International Code of Zoological Nomenclature (Third Edition, 1985) and observe its recommendations The manuscript, including footenotes, references and tables, must be typed with double spacing (30 lines per page) on side A4 paper (210 mm × 297 mm), in duplicate, and should be not longer than 30 pages Pages must be numbered throughout the manuscript Final version (corrected as requested referees and editorial board) is preferably accepted on IBM PC – compatible 5 25"or 3 5" diskette

Heading Title of paper, full name(s) of author(s), place of work with full address – on separate line

Abstract summarizing consisely the contents of the paper and indicating the relevance of the work, should not exceed 20 type-writen lines

Key words Select a set (one or two lines) of key words (index terms)

References Within the text – Dryden (1968), (Latin 1967), Kummari & Nair (1967), Tamiro et al. (1970), the full citation should be given in the list of references Under the References authors should be cited in full followed by abbrevitations of periodical in accordance with The World List of Scientific Periodicals, 4th edition, London Butterworths (1964–1965) The number is to be given (in parentheses) only when individual numbers are paginated independently (see example b) References to papers published in languages other than the major ones, or printed in characters other than Latin, should be content English translation, with an appropriate note at the end (see examples e, f, g, h)

Examples

(a) Dryden G L 1968 Growth and development of Suncus murinus on Guam J Mammal 49 51 62

(b) Lonberg E & Gustavson C 1937. Contribution to the life history of the stripped wrasse. Ark Zool 29(7) 1–16

(c) Lattin G de 1967 Grundriss der Zoogeographie Jena Fischer Verlag, 602 pp

(d) Makin D 1989 The status of bats in Israel. Pp 403-408 In Hanák V, Horáček I & Gaisler J (eds) European Bat Research 1987 Praha Charles Univ Press, 718 pp

(e) Schornikov E I 1969 A new family of Ostracoda from the supralitoral zone of Kuril Islands. Zool Zh 48 494-498 (in Russian, Engl abstr)

(f) Nikolajev G V 1987 Plastinchatousye zhuki (Coleoptera, Scarabaeoidea) Kazakhstana i Srednei Azii [Scarabaeoidaea (Coleoptera) of Kazakhstan and Central Asia]. Alma-Ata Izd Nauka KazSSR, 232 pp (in Russian)

Nikolaev G. V 1987 Plastinčatousye žuki (Coleoptera, Scarabaeoidaea) Kazahstana i Srednej Azii [Scarabaeoidaea (Coleoptera) of Kazakhstan and Central Asia] Alma-Ata. Izd Nauka KazSSR, 232 pp. (in Russian)

(h) Lekeš V 1993· [Macrolepidoptera of the Polabí lowland] Polabska Příroda 4. 19–20 (in Czech).

Illustrations and their captions or legends must form a separate unit Clear technically perfect line drawings and photographs (black-white, glossy) are accepted The original drawing and photograph (one set) should be more than twice as large as when printed and preferably into blocks or plates so that the blocks of drawings or photographs may be uniformly reproduced over the age with the journal Legends to the illustrations should be supplied on a separate sheet of paper References to illustrations and tables in the text Fig 1, Figs 1–2, Plate 1, Fig 1 (for photographic plates), Table 1, Tab 1, Tabs 1–2

Tables including headings and explanations should be on separate sheet of paper, numbered consequently with Arabic numerals

Marking in the manuscript (in light pencil, not in ink or type written) In the text Latin taxa up to generic level – with wavy underling (italics) In the References names of periodicals (not the Latin names of taxa) with wavy underling

Proofs will be sent to authors. One houndred reprints are supplied free of charge Manuscripts of published papers, diskettes and originals of illustrations are not returned unless return requested

Address of the editorial office Acta Soc Zool Bohem , Dr David Král, Viničná 7, CZ–128 00 Praha 2, Czech Republic

CONTENTS

Articles

Bocak L.: A generic revision and phylogenetic analysis of the subtribe Trichalinina (Coleoptera: Lycidae: Metriorrhynchini) 16

Farkač J.: Three new species and new record of *Leistus* from North India and Tibet (Coleoptera: Carabidae, Nebriini) 20

Horak J.: New taxonomic changes in the genus *Glipa* from the Oriental region and descriptions of three new species of the genus *Ophthalmoglipa* (Coleoptera: Mordellidae) 20

Skuhrava M. & Çam H.: A new gall midge species *Asphondylia anatolica* sp. n. (Diptera, Cecidomyiidae) causing galls on *Astragalus lagurus* (Fabaceae) in Turkey 21

Vitner J.: Reproductive biology of the Central European *Aphodius* species with large scutellum (Coleoptera, Scarabaeidae, Aphodiinae) 22

Book review

Cox F. E. G., Kreier J. P. & Wakelin D. 1998: Parasitology – by J. Jíra 22

Podávání novinových zásilek povoleno Ředitelstvím pošt v Praze č. j. NP 1176/1994 ze dne 13. 6. 1994.